NEW CRETACEOUS BERYCOID FISHES FROM THE LEBANON

BY

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CONTENTS

SYNOPSIS

This paper contains descriptions of four berycoids, three from the Cenomanian fish beds of Hakel and Hajula, *Lissoberyx* gen. nov. *dayi* (Smith Woodward) (Trachichthyidae), *Stichocentrus liratus* gen. et sp. nov. and *Caproberyx pharsus* sp. nov. (both Holocentridae), and one from the Upper Senonian beds of Sahel Alma, *Gnathoberyx stigmosus* gen. et sp. nov. (Trachichthyidae). *Lissoberyx dayi* is the most primitive berycoid yet known, and lies near the origin of the sub-order. *Acrogaster anceps* Arambourg is probably a second species of *Lissoberyx*. *Gnathoberyx* is the only acanthopterygian yet discovered in which a toothed maxilla is the dominant bone in the upper jaw. A new subfamily Caproberycinae is made for the Cretaceous Holocentridae, which do not appear to be ancestral to the Tertiary and living subfamilies. These and other points are considered in a discussion of the origin and early evolution of the Berycoidei. Preliminary observations on the fish beds at Hakel suggest that they were deposited in a sub-marine canyon or gully, the abundance of fishes being due to mass mortalities caused by " waterbloom ". It is suggested that the fish beds at Hakel and Hajula are of Middle Cenomanian age rather than Upper Cenomanian.

I. INTRODUCTION

IN the spring of 1964 I spent a month in the Lebanon, collecting Upper Cretaceous fishes and examining the very large collection of these fishes in the Geology Department of the American University, Beirut. This paper is the first of a series dealing with new material resulting from this trip. It contains preliminary discussions of the palaeoecology and age of the Cenomanian fish beds of the Lebanon, and descriptions of four berycoid fishes, three of them representing new genera.

It is a pleasure to acknowledge here all the help I received in the Lebanon, in particular from Prof. Theodore Raven, Geology Department, American University,

Beirut, who gave me every facility and allowed me to borrow specimens from the collection in his care.   My thanks are also due to Mrs. Raven, to Mr. Bud Young of the Geology Department and Dr. Karl George of the Zoology Department in the American University, and especially to my friends Mr. & Mrs. I. N. H. Seymour of Beirut.   I am also most grateful to Dr. D. D. Bayliss for his comments on the microfauna of the Lebanon fish beds, to Mr. C. I. Macadie for his help in preparing the specimens, and to Mr. N. Tanti, who photographed the fishes.

The material described here is in the collections of the British Museum (Natural History), identified by the prefix " P." before the registered number, and the Geology Department of the American University, Beirut, referred to by " AUB " before the number.

II. LOCALITIES AND CONDITIONS OF DEPOSITION

The fishes described here are from the three classic fish localities in the Lebanon, Hakel, Hajula (both Cenomanian in age) and Sahel Alma (Upper Senonian).   I was unable to visit Sahel Alma and have nothing to add to published information on the locality (Roger, 1946 ; Dubertret, 1963 : 119 ; Patterson, 1964 : 365 and references cited there).   At Hakel and Hajula, two villages about 4 km. apart, at about 700 m., respectively 11 and 9 km. inland from Byblos (Jebail), the fish beds are very similar in age and fauna (Roger, 1946 ; Dubertret, 1963 : 57 ; Patterson, 1964 : 362 and references cited there).   Although much has been published on the fauna of Hakel and Hajula, knowledge of the conditions under which the beds were deposited rests on Roger's monograph (1946) which dealt with the invertebrates of all three localities and gave particular attention to the palaeoecology.   Roger had not visited the Lebanon and described the fauna of Hakel as being from two localities, Hakel and Maifouk (a neighbouring village), when only one exposure of fish beds exists there (Dubertret, 1963 : 58).   Roger concluded (p. 83) that the Cenomanian fish beds were laid down as soft, fine mud on a deoxygenated bottom in channels between shallows supporting reefs of rudists, well clear of coasts.   He visualized the rocks as being deposited in several hundred metres of water, basing this estimate on the crustacean fauna and the similarity of the rocks to *Globigerina* ooze.

Further fieldwork is necessary before a detailed account of the palaeoecology of the Cenomanian fish beds can be given, but some preliminary observations are worth mentioning here.   At Hajula the exposure is in the centre of the village and building, cultivation and the inhabitants prevented me from forming an accurate estimate of the extent and thickness of the fish beds, but at Hakel the beds are well exposed in a narrow valley, in dip on the southern side and in strike on the northern, the beds dipping to the north at about 30°.   The exposure is about 250 m. long (east–west) and about 200 m. broad (north–south).   On the south side of the valley blasting was carried out in the centre of the exposure about six years ago.   The fish beds are at least 20 m. thick and their base has not been seen : above they pass into flaggy, unfossiliferous limestones.   The fish beds consist of thin-bedded, siliceous limestones alternating irregularly with more massive limestones.   Occasional nodules and lenses of impure chert occur throughout the beds.   The rock is normally pale buff in colour, but bluish and grey beds occur occasionally, the former mainly in the massive

limestones, the latter in the thin-bedded. Under the hammer the rock often gives off a bituminous smell, as Roger (1946 : 76) noted. From museum collections one gains the impression that the bedding planes are flat and smooth, but in fact there is a great deal of complex small scale folding in the thinner beds, probably due to slumping in the unconsolidated sediment. This suggests that the fish beds were deposited on a slope. Apart from these contorted beds, the bedding planes are flat and I have seen no ripple marks nor any signs of current bedding or graded bedding.

At each end of the exposure the fish beds terminate abruptly against massive, structureless and unfossiliferous limestones. These junctions are not faulted as earlier authors have thought, for higher in the valley wall beds pass across the line of junction without interruption. At the junction the fish beds are slightly contorted and shattered, tending to bend upwards, but there is no sign of any breccia or conglomerate. The line of junction is steeply inclined outwards (away from the centre of the exposure) at both ends of the fish beds, but where the junction is best exposed, in the stream bed at the eastern end of the exposure, the fish beds appear to undercut the massive limestone. Two possible explanations of this contact present themselves : the first that the massive limestones are a reef, evidently entirely recrystallized since no fossils or structures are preserved ; the second that the limestones are the walls of a submarine canyon or gully. The following points, each of which is difficult to reconcile with deposition close to a reef (indicating shallow, well oxygenated water), suggest that the second of these interpretations is preferable :

(i) the high organic content and bituminous smell of the fish beds, together with the complete absence of sessile benthos, indicating a deoxygenated bottom.

(ii) the absence of any reef breccia at the contact between the massive limestones and the fish beds.

(iii) the microfauna of the fish beds consists of abundant radiolarians, moderately abundant pelagic Foraminifera (*Hedbergella*) and rare benthonic Foraminifera (textulariids) : my colleague Dr. D. D. Bayliss, who kindly examined thin sections of the fish beds and identified the Foraminifera, considers the rock to be a foraminiferan/radiolarian ooze, suggesting near bathyal depths.

As a preliminary hypothesis, it is therefore suggested that the Cenomanian fish beds of Hakel were laid down in a submarine canyon or gully which in some way served as a trap for fishes and invertebrates which were preserved in large numbers because of the deoxygenated bottom and a supply of fine sediment. Further, the extreme abundance of well-preserved fishes and crustaceans through many metres of rock, some of the bedding planes being completely covered by fishes, is clear evidence of the occasional occurrence of mass mortalities. As a further hypothesis I would propose that these mass mortalities were caused, like the majority of known examples (Brongersma–Sanders, 1957), by toxins released in " waterbloom " conditions, and that the high percentage of silica in the rocks (21% at Hakel, not detrital but colloidal, Roger, 1946 : 77) results from the solution of diatom frustules.

III. THE AGE OF THE CENOMANIAN FISH BEDS

The age of the beds at Hakel and Hajula, though known to be Cenomanian, is not yet precisely fixed stratigraphically but estimated from the fish faunas. d'Erasmo

(1946 : 134) and Arambourg (1954 : 163) both concluded that an Upper Cenomanian age is most probable, and in an earlier paper (Patterson, 1964 : 362) I accepted this estimate. d'Erasmo's conclusion was based on a comparison with the fauna of Comen, near Trieste : he thought that both faunas were Upper Cenomanian in age. Arambourg, describing the fauna of Jebel Tselfat, Morocco, found that it is closest to that of Comen, and that since Comen and Jebel Tselfat share certain archaic genera (*Belonostomus, Thrissops, Clupavus*) which are absent at Hakel and Hajula they are probably Lower Cenomanian in age while the Lebanese localities are Upper Cenomanian. Some new evidence suggests that a re-examination of these conclusions is necessary. The microfauna of Hakel (*Hedbergella* present, no *Globotruncana* or *Rotalipora*) suggests an age low in the Cenomanian according to Dr. D. D. Bayliss (personal commn.), and Dubertret (1963 : 57) speaks of the fish beds at Hakel and Hajula as lying low in the Cenomanian. The more advanced teleosts suggest close relationship between the Lebanese fauna and that of Jebel Tselfat : *Protobrama* (Hajula) is close to *Tselfatia* (Jebel Tselfat) (Patterson, 1967 : 230), *Caproberyx* is present at both Hakel and Jebel Tselfat (p. 98) and *Lissoberyx dayi* (Hakel & Hajula) resembles *Acrogaster anceps* (Jebel Tselfat) (p. 79). Further, one cannot attach much importance to the presence at Comen and Jebel Tselfat of *Belonostomus, Thrissops* and *Clupavus*, which Arambourg holds to be archaic forms absent at Hakel and Hajula. *Belonostomus* occurs rarely at Hakel (P.4029, P.8676) and in any case is of little value as an indicator of age since it ranges upwards to the Maestrichtian. Although *Thrissops* is apparently absent at Hakel and Hajula, *Eubiodectes* (Hay, 1903 : 415) is very similar and possible synonymous (Bardack, 1965 : 35). As I hope to show in a forthcoming paper, *Clupavus* or a related genus is abundant at Hakel and Hajula, although not previously recognized : the species *Clupea gaudryi* Pictet & Humbert (1866 : 60, pl. 5, figs. 2–5) is not a *Scombroclupea* as Smith Woodward (1901 : 138), Kramberger (1895 : 37), d'Erasmo (1922 : 72 ; 1946 : 70) and other authors have supposed since the type material lacks ventral scutes and finlets behind the anal fin. The specimens described as *Scombroclupea gaudryi* by Smith Woodward, d'Erasmo and Kramberger are true *Scombroclupea* but are not conspecific with the type material, which is close to *Clupavus*.

But in spite of this evidence of relationship with the faunas of Comen and Jebel Tselfat, Hakel and Hajula contain some advanced groups which are absent in the Moroccan and Dalmatian localities. The most important of these are the primitive eels (*Urenchelys, Anguillavus* and possibly *Enchelion*) and the Ctenothrissiformes (*Ctenothrissa* and *Pateroperca*). These two groups occur otherwise only in the English Chalk (with the exception of a species of *Anguillavus* in the Kansas Chalk (Martin, 1920 : 95, pl. 6)), whose lower zones are definitely of Upper Cenomanian age. But the Lebanese fauna is almost certainly older than that of the Upper Cenomanian zones of the English Chalk, for it lacks groups such as the specialized ichthyodectids (*Ichthyodectes, Xiphactinus*) which are present there, and contains primitive forms (Clupavidae, *Diplomystus brevissimus*) absent in the Chalk.

In summary, the fauna of Hakel and Hajula is closely related to that of Comen and Jebel Tselfat, Lower Cenomanian in age, but is probably younger than these (eels and ctenothrissoids present). It is also closely related to the fauna of the

Upper Cenomanian zones of the English Chalk, but is probably older than this (clupavids and *Diplomystus brevissimus* present, no advanced ichthyodectids). Pending more precise stratigraphic work in the Lebanon, a Middle Cenomanian age seems most likely for Hakel and Hajula.

IV. SYSTEMATIC DESCRIPTIONS
Order BERYCIFORMES

DIAGNOSIS. See Tate Regan (1911 : 2).

Suborder BERYCOIDEI

DIAGNOSIS. See Patterson (1964 : 433).

Family **TRACHICHTHYIDAE** Bleeker 1895

DIAGNOSIS. See Patterson (1964 : 305).

Genus *LISSOBERYX* nov.

DIAGNOSIS. Small Cretaceous Trachichthyidae with the bones of the head without ornament except for weak serrations on the edges of the infraorbitals, preopercular, interopercular and subopercular ; skull roof broad and flat, without ornament, crests or mucus cavities ; supraoccipital crest short and high, supratemporal fossa ending above posterior edge of orbit ; post-temporal fossa partially roofed ; toothless maxilla expanded posteriorly, two supramaxillae, ectopterygoid toothed ; opercular covered by scales ; 23 vertebrae including one ural centrum ; dorsal fin with 5 spines, anal with 4, less than 10 soft rays in each ; scales thin and ctenoid, none enlarged, no ventral ridge scales.

TYPE SPECIES. *Acrogaster dayi* Smith Woodward, 1942.

Lissoberyx dayi (Smith Woodward)
(Pl. 1, fig. 1, Pl. 4, fig. 1 ; Text-figs. 1–3)

1942 *Acrogaster dayi* Smith Woodward : 540, pl. 4, fig. 2.
1964 *Acrogaster dayi* Smith Woodward ; Patterson : 410.

DIAGNOSIS. As for genus, only species : reaching about 4 cm. in standard length ; D V, 9 ; A IV, 8 ; P c. 10 ; V I, 6.

HOLOTYPE. AUB 108930, Day colln., American University, Beirut.

MATERIAL. In addition to the holotype, four specimens, AUB 101997, 107578, 108926 and 109129, Day colln., American University, Beirut.

HORIZON AND LOCALITIES. Middle Cenomanian ; Hajula (4 specimens) and Hakel (1 specimen), Lebanon.

DESCRIPTION. Smith Woodward's original description (1942 : 540) mentions nothing except the proportions of the trunk and the composition of the dorsal and anal fins. The description which follows is based mainly on AUB 107578 (Pl. 4,

fig. 1) and 108926 (Pl. I, fig. 1) which have been prepared with acid after embedding in resin. Text-figures 1–3 are composite restorations, based on four specimens.

Measurements and proportions. The dimensions of the five specimens are shown in Table 1.

TABLE 1.—Dimensions (in mm.) of specimens of
Lissoberyx dayi (Smith Woodward)

Specimen	Total length	Standard length	Maximum depth	Length of head	Predorsal length	Preanal length
AUB 108930*	48	41	22	16	24	30
,, 101997	32	26	14	12	13	23
,, 107578	—	—	13	10	13	20
,, 108926	40	34	16	15	17	28
,, 109129	44	39	20	15	21	30
mean % standard length	118%	100%	49%	42%	53%	80%

* Corrected measurements from Smith Woodward's figure (1942, pl. 4, fig. 2) of the holotype, which is not natural size as stated but × c. 1·2.

Lissoberyx dayi was a small, deep-bodied fish (Text-fig. 3) reaching about 40 mm. in standard length, 50 mm. in total length. The maximum depth of the trunk is almost exactly half the standard length, the length of the head about 42% of the standard length.

Neurocranium. No details of the basicranium are visible in any specimen but the skull roof (Text-fig. 1) is moderately well exposed in the two acid prepared specimens, although few of the sutures can be seen. The skull roof is short and very broad. It is unlike that of any living berycoid in being quite smooth, without the strong ornament characteristic of the holocentrids or the crests and mucus cavities of the trachichthyids and their relatives. There is a high, triangular supraoccipital crest (*soc.*), thickened anteriorly, which rises from a short, broad supratemporal fossa (*st. f.*). The supratemporal fossa is limited anteriorly and laterally by a low, smooth crest, formed by the frontals anteriorly and the parietals (*pa.*) laterally. The dorsal limb of the extrascapular (*ext.*) articulated with the hind end of the parietal crest and a short groove on the medial face of the crest carried the terminal part of the supratemporal commissural sensory canal, as in many fossil and living berycoids. The limits of the parietals, epiotics and supraoccipital within the supratemporal fossa cannot be distinguished. Lateral to the supratemporal fossa there is a high, narrow post-temporal fossa (*pt. f.*). The post-temporal fossa is partially roofed by the parietal and pterotic (*pto.*), which make contact in the lateral wall of the fossa (108926), as in other Cretaceous berycoids (*Hoplopteryx, Trachichthyoides, Caproberyx pharsus* : Patterson 1964 : 360, text-figs. 47, 55 : p. 98). This contact between the parietal and pterotic is a relic of the complete roof of the post-temporal fossa in more primitive teleosts. Lateral to the post-temporal fossa the pterotic projects in a broad, smooth wing, continued anteriorly by the sphenotic (*spo.*). On the lower margin of the
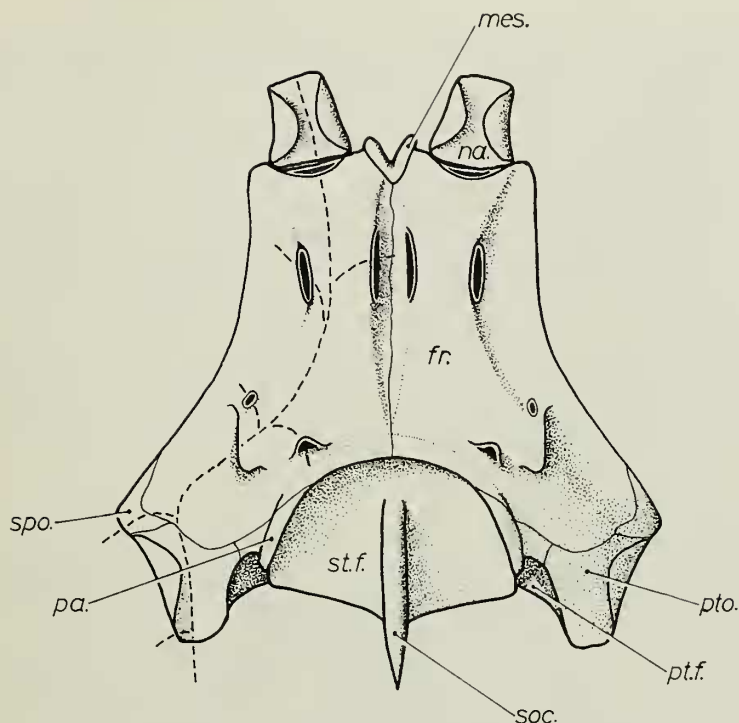
FIG. 1. *Lissoberyx dayi* (Smith Woodward). Restoration of the skull roof in dorsal view, ×8 approx. *fr.*, frontal; *mes.*, mesethmoid; *na.*, nasal; *pa.*, parietal; *pt.f.*, post-temporal fossa; *pto.*, pterotic; *soc.*, supraoccipital; *spo.*, sphenotic; *st.f.*, supratemporal fossa. The broken line on the left side of the figure indicates the course of the sensory canals.

exposed area of the pterotic there is a flange projecting dorsally : this flange carried the main cephalic sensory canal on its dorsal surface, the infraorbital and preopercular canals passing ventrally before and behind it respectively. Below the flange there is a moderately deep dilatator fossa. An exactly similar flange is present in the living holocentrid *Myripristis*.

The major part of the skull roof is formed by the frontals (*fr.*), the two bones together covering an area about as broad as it is long. Each frontal has a broad, smooth supraorbital flange passing back to its junction with the sphenotic. The supraorbital sensory canal, passing on to the frontal from the sphenotic, entered the bone at the level of the front of the supratemporal fossa through an elongated opening covered by a projecting flange of bone. A small pore just in front of this opening transmitted a short branch of the canal on to the supraorbital flange, and a postero-medial branch opened through a larger pore, again covered by a projecting flange, at the foot of the crest bounding the supratemporal fossa. The canal passed to the anterior end of the frontal in a wide tube which opens through two elongated

pores above the anterior third of the orbit, one leading laterally on to the supra-orbital flange, the other opening into a long, shallow median depression between the frontals. This simple, largely enclosed canal system resembles that in holocentrids like the living *Holocentrus* and *Myripristis* and the Cretaceous *Stichocentrus* and *Caproberyx* (Text-figs. 7, 10) ; it is quite unlike the system of open mucus cavities found in the trachichthyids and their allies. From a wide opening in the anterior edge of the frontal the supraorbital canal passed forwards to the nasal (*na.*). The nasals are moderately large, smooth bones, tapering forwards, with the lateral and medial edges rolled upwards to form a partially enclosed channel for the sensory canal. The nasals were loosely attached to the frontals, not sutured on as they are in most trachichthyids.

Enclosed between the anterior ends of the frontals is the " V " shaped upper edge of the mesethmoid (*mes.*). The lateral ethmoids (*l.e.*) are deep and very broad. The parasphenoid is deep, broad and without teeth. The vomer is not visible in any specimen, nor can an orbitosphenoid be seen.
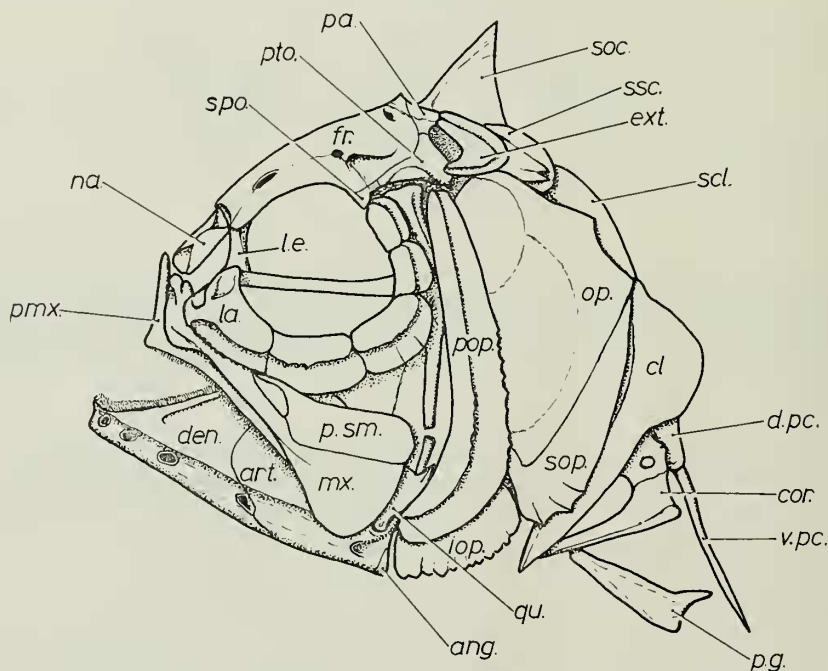
Fig. 2. *Lissoberyx dayi* (Smith Woodward). Restoration of the skull and pectoral and pelvic girdles in left lateral view, ×5 approx. *ang.*, angular ; *art.*, articular ; *cl.*, cleithrum ; *cor.*, coracoid ; *den.*, dentary ; *d.pc.*, dorsal postcleithrum ; *ext.*, extra-scapular ; *fr.*, frontal ; *iop.*, interopercular ; *la.*, lachrymal ; *l.e.*, lateral ethmoid ; *mx.*, maxilla ; *na.*, nasal ; *op.*, opercular ; *pa.*, parietal ; *p.g.*, pelvic girdle ; *pmx.*, premaxilla ; *pop.*, preopercular ; *p.sm.*, posterior supramaxilla ; *pto.*, pterotic ; *qu.*, quadrate ; *scl.*, supracleithrum ; *soc.*, supraoccipital ; *sop.*, subopercular ; *spo.*, sphenotic ; *ssc.*, suprascapular ; *v.pc.*, ventral postcleithrum.

Circumorbital bones. The infraorbital series contains the normal complement of four infraorbitals and a lachrymal. All the infraorbitals are deep (Text-fig. 2), with a deep flange overhanging the groove for the sensory canal. There are a few weak serrations on the edge of this flange on the first and second infraorbitals and two shallow grooves marking branches of the canal on the second infraorbital : the bones are otherwise smooth. There is a broad subocular shelf on the second infraorbital only. The lachrymal (*la.*) is no deeper than the infraorbitals ; dorsally it articulates with the lateral ethmoid by a strong facet. The groove for the sensory canal on the lachrymal is bridged by a bar of bone where it turns upwards anteriorly, and there are a few weak serrations on the ventral edge of the bone. There is no trace of an antorbital but the apparent absence of this small bone could be due to imperfect preservation.

Palate and jaws. The hyomandibular lies almost vertically and is slender, with an undivided head. The symplectic inclines forwards slightly and the condyle of the quadrate (*qu.*) lies below the hind edge of the orbit. The endopterygoid is not toothed. The ectopterygoid is toothed, and although the palatine is not visible in any specimen it will almost certainly have borne teeth, since I know of no acanthopterygian in which a toothed ectopterygoid occurs with a toothless palatine.

The ascending process of the premaxilla (*pmx.*) is about half as long as the toothed alveolar process and is well marked off from the articular process. The maxilla (*mx.*) is about half as long again as the premaxilla and strongly expanded posteriorly, but there are no teeth on the posterior expansion as there are in *Myripristis* and the Cretaceous *Hoplopteryx macracanthus* (Patterson, 1964 : 334) and *Gnathoberyx* (p. 83). There are two supramaxillae, the posterior (*p. sm.*) with a slender process overlying the anterior. The mandible is long and deep, both the dentary (*den.*) and the articular (*art.*) forming a high coronoid process, that of the dentary toothed throughout its length. At the symphysis the band of teeth on the dentary becomes broader but does not extend on to the lateral face of the bone as it does in some berycoids. At the back of the mandible there is a very small angular (*ang.*). The mandibular sensory canal ran in a closed tube opening by three pores in the dentary and a pore at the suture between dentary and articular. All the bones of the jaws are without ornament.

Opercular bones. The preopercular (*pop.*) is long, broad, inclined backwards a little and weakly angulate. There are weak serrations on the posterior edge of the lower half of the vertical limb and a few serrations above the angle in the bone on the edge of the flange overhanging the groove for the sensory canal. The opercular (*op.*) is smooth, but has two weak spines on its posterior edge. The opercular is covered by scales : two very large cycloid scales cover the anterior part of the bone with three or four smaller scales on the posterior part (101997, 107578). The subopercular (*sop.*) has the normal spike overlapping the ventral corner of the opercular, and three ridges, each ending in a serration, on its ventral edge. The interopercular (*iop.*) bears a number of weak ridges ending in feeble serrations along its ventral edge.

Hyoid arch and branchiostegals. The ceratohyal is ossified in the usual two pieces ; the distal ossification is very deep and is perforated by a large oval fenestra. There are seven branchiostegals, three articulating with the medial face and two with the

lateral face of the distal ceratohyal, and two articulating the lateral face of the proximal ceratohyal.

Vertebral column. There are 23 vertebrae, 9 abdominal and 14 caudal, including one free ural centrum (the second). Ribs are present on all the abdominal vertebrae except the first, and are borne on transverse processes on the last four (five in 101997). There are no epineurals or epipleurals. The caudal skeleton will not be described in detail here since I am dealing with the caudal skeletons of all Cretaceous Beryciformes in a forthcoming paper : suffice it to say that the caudal of *Lissoberyx* agrees with that of the living trachichthyid *Hoplostethus* (Gosline, 1961 : 14) in having a neural crest on the second pre-ural centrum and a free second ural centrum.

Pectoral and pelvic girdles and fins. The pectoral girdle contains the normal complement of bones, a curved extrascapular (*ext.*) articulating with the parietal
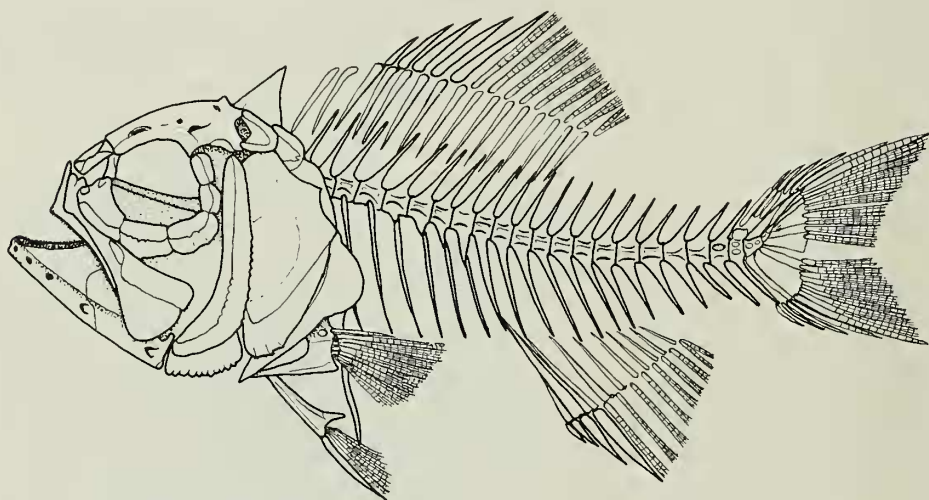

FIG. 3.   *Lissoberyx dayi* (Smith Woodward).   Restoration of the skeleton, scales omitted, × 2·5 approx.

above and the pterotic below, a forked suprascapular (*ssc.*) articulating with the epiotic and intercalar, a blade-shaped supracleithrum (*scl.*), a large, sigmoid cleithrum (*cl.*), two post-cleithra, the upper (*d. pc.*) scale-like, the lower (*v. pc.*) rod-like, and the scapula and coracoid. All the dermal bones of the girdle are smooth and unornamented. The anterior process of the coracoid (*cor.*) is moderately stout and long, arching forwards to join the cleithrum just above its tip. The pectoral fin contains about ten rays.

The pelvic fins are thoracic, the fin originating well in front of the tip of the ventral post-cleithrum and the girdle (*p. g.*) ending between the anterior processes of the coracoids. The pelvic fin contains a stout, smooth spine and six soft rays.

Median fins. The dorsal fin originates above the pelvic and occupies little more than half the back of the fish ; it contains five smooth spines, increasing in length from front to rear, and 9 soft rays. The longest spine is equal in length to the

distance between the base of the fin and the vertebral column. The first radial of the fin is not enlarged, and lies between the neural spines of the second and third vertebrae. There are two predorsals (Smith & Bailey, 1961) in front of the fin. The anal fin arises below the hind end of the dorsal ; it contains four spines, increasing in length, and 8 soft rays. The fourth anal spine is equal in length to the fifth dorsal spine. The first anal radial is very small and the second is only a little enlarged.

The forked caudal fin contains 19 principal rays with 17 branched, 9 in the upper lobe and 8 in the lower. Preceding the upper lobe there are four small spines and one segmented ray, preceding the lower three spines and a segmented ray.

Squamation. The scales are large, thin and coarsely ctenoid. There are 13 scales in a transverse series on the trunk, the lateral line passing through the fifth from the top. The lateral line scales are not enlarged. Scales cover the cheek and the opercular, but the scales do not extend over the bases of the fins. There are no ventral ridge scales.

AFFINITIES. Smith Woodward (1942 : 540), in his original brief description of *Lissoberyx dayi*, placed the species in the trachichthyid genus *Acrogaster*. Clearly the species cannot be included in this genus : in *Acrogaster* the skull roof bears a normal trachichthyid system of large mucus cavities separated by high, serrated crests, the alveolar process of the premaxilla is almost as long as the maxilla and the maxilla is not expanded behind it, the preopercular bears a number of large spines at the angle, there are no scales on the operculum, there are eight branchiostegals and the scales are cycloid (Patterson, 1964 : 410). In all these characters *A. dayi* differs from the Senonian species of the genus, and since it shows no signs of close relationship with any other Cretaceous genus it is necessary to make a new genus to receive it. The name *Lissoberyx* refers to the smooth skull roof and general absence of ornament on the head. *Acrogaster anceps* Arambourg (1954 : 153), known by a single specimen from the Lower Cenomanian of Morocco, is probably another species of *Lissoberyx* : it agrees with *L. dayi* and differs from the Senonian species of *Acrogaster* in having the maxilla expanded posteriorly, in the small number of vertebrae (21) and in the form of the dorsal and anal fins. Through the kindness of Prof. J. P. Lehman and Mlle. J. Signeux I was able to examine this specimen and could find no trenchant differences from *L. dayi*. Although Arambourg found traces of two or three spines on the angle of the preopercular he spoke of these as " assez fruste " : to me it appears that these traces are not spines but ridges on the surface of the bone marking branches of the sensory canal. Arambourg described the pelvic as containing 7 or 8 soft rays, a difference from *L. dayi* and all trachichthyids, but in my opinion the pelvic fins are not sufficiently well preserved for an accurate count to be made.

That *Lissoberyx dayi* is a member of the Beryciformes is shown by the presence of fin spines, pelvics with more than five soft rays, two supramaxillae and a nineteen-rayed tail. Within the Beryciformes *Lissoberyx* falls in the sub-order Berycoidei (Patterson 1964 : 433) because of the toothless endopterygoid, the absence of epineurals, the pelvic spine and the nineteen-rayed caudal. All known Cretaceous Berycoidei are members either of the Trachichthyidae or the Holocentridae, and there is normally no difficulty in deciding to which of these two families a genus

belongs. However, as the Trachichthyidae and Holocentridae are traced back to the Cenomanian they begin to converge, holocentrid characters such as maxillary teeth and an antorbital appearing in the trachichthyid *Hoplopteryx* and trachichthyid characters such as a small number of dorsal fin spines, a large supraoccipital crest and a supratemporal fossa appearing in the holocentrid *Caproberyx* (Patterson, 1964 : 341, 359 ; p. 102). In *Lissoberyx* this trend goes further : the fish is a mosaic of trachichthyid and holocentrid features.

First, there are several characters of *Lissoberyx* which are common to both trachichthyids and holocentrids in the Cretaceous, though not always to living members of these families. These include the partial roof over the post-temporal fossa (as in *Hoplopteryx*, *Trachichthyoides* and *Caproberyx pharsus*, p. 98), the presence of ectopterygoid teeth, two supramaxillae (only one in living trachichthyids), the mandibular sensory canal running in a canal opening by three or four pores (as in Cretaceous but not living holocentrids), the preopercular without a spine at the angle, the deep, perforate ceratohyal (as in Cretaceous but not in living holocentrids), the presence of predorsals in front of the dorsal fin and the insertion of the first dorsal radial between the second and third neural spines (as in *Hoplostethus* and living holocentrids), the four anal fin spines and the unmodified anal radials (the third anal spine is enlarged in most holocentrids, but not in *Caproberyx*) and the unspecialized ctenoid scales.

Secondly, there is a group of characters in which *Lissoberyx* resembles the trachichthyids and differs from the holocentrids. These include the high supraoccipital crest and moderately large supratemporal fossa (a similar supraoccipital crest occurs in the holocentrids *Caproberyx* and *Stichocentrus*, Text-figs. 8, 10, but there the supratemporal fossa is much smaller), the deep infraorbitals with the lachrymal no deeper, the subocular shelf on the whole of the second infraorbital (as in *Hoplopteryx* but not in living trachichthyids), the 23 vertebrae (the vertebral number never seems to fall below 26 in holocentrids), the six soft rays in the pelvic fin (7 in holocentrids except in *Caproberyx pharsus*, p. 102), and the form of the dorsal fin, with five spines and nine soft rays (no holocentrid is known to have less than six spines and eleven soft rays).

Thirdly, characters in which *Lissoberyx* resembles the holocentrids and differs from the trachichthyids include the absence of large mucus cavities on the skull roof and the pattern of the supraorbital sensory canal (as in *Myripristis*), the form of the pterotic (again as in *Myripristis*), the nasals not sutured to the frontals or to each other, the unreduced mesethmoid, the short alveolar process of the premaxilla and the strongly expanded maxilla, the presence of scales on the operculum (though in Cretaceous holocentrids only the antero-dorsal corner of the opercular is scaly), and the rather long and stout anterior process of the coracoid.

Finally, there are a few characters in which *Lissoberyx* differs from both the trachichthyids and the holocentrids. These are the smoothness of the skull roof and the almost complete absence of ornament on the bones of the head, the seven branchiostegal rays (eight in both trachichthyids and holocentrids) and the complete scaly covering of the opercular.

Evaluation of this complex of characters is difficult : the characters in each group

cannot simply be counted because they obviously differ in significance.   On balance, I feel sure that *Lissoberyx* lies nearer to the trachichthyids than to the holocentrids, particularly significant associations with the trachichthyids being the supratemporal fossa, the form of the infraorbitals, the number of vertebrae and the dorsal and pelvic fins.   But the most important features in which *Lissoberyx* resembles the holocentrids, the characters of the skull roof and the upper jaw, are almost certainly primitive, since the deep mucus cavities of the trachichthyid skull roof can hardly be anything but specialized and since a short premaxilla and an expanded maxilla are more likely to be primitive than a premaxilla extending to the tip of the maxilla (Patterson, 1964 : 439).   Of the characters in which *Lissoberyx* differs from both holocentrids and trachichthyids, the smooth skull roof and absence of ornament on the head must be primitive while the seven branchiostegals are advanced.   The scaly opercular is probably primitive for the berycoids (see below p. 107).   It may be significant that in the seven branchiostegals and the scaly opercular (as also in the lack of ornament and the unreduced mesethmoid) *Lissoberyx* resembles the Berycidae (particularly *Beryx*), a group probably derived from the trachichthyids.

The presence of ribs on all but the first abdominal centrum in *Lissoberyx* is a peculiar feature which is otherwise known only in *Stichocentrus* (p. 93) among Beryciformes.   In acanthopterygians the first two vertebrae normally bear only slender bones which appear to be in series with the epipleurals rather than the ribs (Starks, 1904 : 616 ; Gosline, 1963 : 28).   It may be that in *Lissoberyx* an anterior centrum has become incorporated in the neurocranium, but the fact that the first dorsal radial lies between the second and third neural spines in *Lissoberyx*, *Hoplostethus*, *Stichocentrus* and living holocentrids suggests that the first free vertebra is homologous in all these forms.   It is also possible that the slender bones borne on the first two vertebrae of some acanthopterygians are not epipleurals but reduced ribs : the skeletons of living Beryciformes that I have examined suggest that this may be true of trachichthyids and some holocentrids.   In any event, Rosen (1964 : 242) shows that differences in the point of origin of the first rib cannot be interpreted in the simplest terms in teleosts.

In summary, *Lissoberyx* is a trachichthyid, but it shows more resemblance to the holocentrids than any other trachichthyid and must lie very close to the common stock of these two families and of the sub-order Berycoidei.   As the most generalized member of this sub-order, *Lissoberyx* throws some light on the origin of the group and is discussed further on p. 106 below.

Genus *GNATHOBERYX* nov.

DIAGNOSIS.   Small Cretaceous Trachichthyidae in which the maxilla is toothed and forms more than half the gape ; superficial bones of the head and scales spiny ; long, slender teeth in the upper jaw, supramaxillae reduced or absent ; 27 vertebrae, including a free second ural centrum ; dorsal and anal fin each with four spines and less than ten soft rays ; scales ctenoid and spiny, lateral line scales enlarged and thickened, ventral ridge scales present.

TYPE SPECIES.   *Gnathoberyx stigmosus* sp. nov.

Gnathoberyx stigmosus sp. nov.

(Pl. 1, fig. 2, Pl. 2 ; Text-figs. 4, 5)

DIAGNOSIS.   As for genus, only species : reaching about 4 cm. in standard length, depth of trunk about 45% of standard length, length of head about 35% of standard length ; D IV, 9 ; A IV, 8.

HOLOTYPE.   AUB No. 100402 (Pl. 1, fig. 2, Pl. 2, fig. 2).

MATERIAL.   In addition to the holotype, AUB No. 103838 (Pl. 2, fig. 1).

HORIZON AND LOCALITY.   Upper Senonian ; Sahel Alma, Lebanon.

DESCRIPTION.   Acid preparation has not been used on this species because there are only two specimens and material from Sahel Alma often gives poor results in transfer preparations.   For this reason much of the cranial anatomy remains unknown at present.

Measurements and proportions.   The dimensions of the two specimens are as follows (in mm.), the first figure in each case being for the holotype, the second for 103838 : total length : 50–52, standard length : 40–c. 42, maximum depth of trunk : c. 20–18, length of head : 16–15, predorsal length : 21–23, preanal length : c. 28–27.

Although both specimens are distorted, 103838 by oblique crushing, the holotype by displacement of the anal fin and deepening of the trunk, they are clearly closely comparable in size.   *G. stigmosus* was a small, deep-bodied fish, about 40 mm. in standard length, with the maximum depth of the trunk about 46% of the standard length and the length of the head about 35% of the standard length.

Neurocranium.   The skull roof is not well exposed in either specimen.   The supraoccipital crest was low, not projecting above the skull roof, and apparently
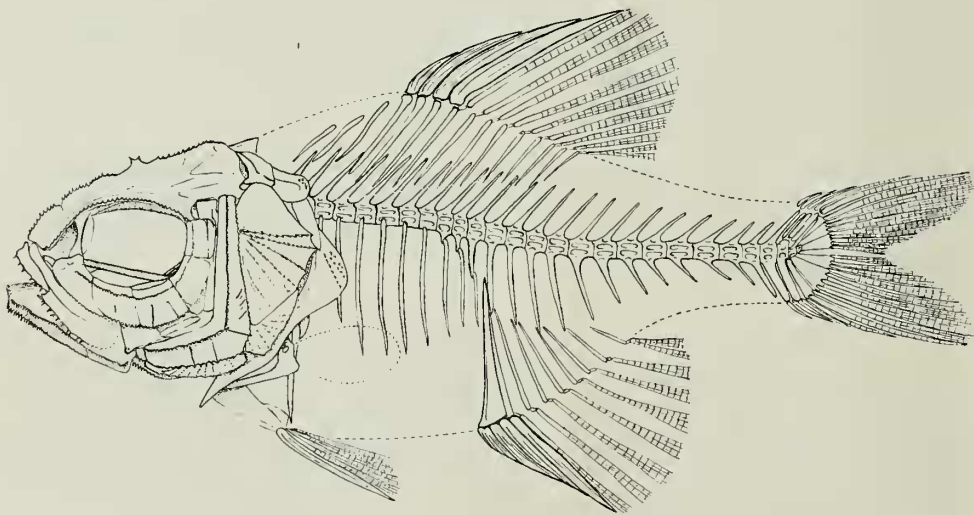

FIG. 4.   *Gnathoberyx stigmosus* gen. et sp. nov.   Restoration of the skeleton, scales omitted, × 2·5 approx.

rather short, arising at the level of the hyomandibular facet. The skull roof bore a pattern of high crests bounding mucus cavities, as is normal in trachichthyids, but the details of the pattern cannot be made out. The lateral margin of the frontal above the orbit bears a row of large, pointed spines and there is a more medial crest bearing similar spines which is continued back by the parietal. The postero-lateral part of the skull roof is smooth and without ornament. The nasals are large, thick, scroll-like bones, probably sutured to the frontals, with coarse spines on their margins. The nasals extend antero-ventrally almost to the vomer, indicating that in this species, as in *Hoplopteryx* and living trachichthyids, the mesethmoid was much reduced. These facts suggest that the skull roof of *Gnathoberyx* was of the same type as in *Hoplopteryx* and *Hoplostethus* (Patterson, 1964, text-figs. 46, 54, 65), and that the supratemporal fossa was short, as in Trachichthyidae, not extended forwards as it is in Berycidae.

An orbitosphenoid is not visible in either specimen. The parasphenoid is straight and slender, and there is a long basisphenoid pedicel articulating with it at the hind edge of the orbit. No details of the otic region are visible.

Infraorbital bones. The infraorbitals are very deep, as deep as or deeper than the lachrymal. Dorsally they bear a thickened, serrated flange projecting over the groove for the sensory canal and the ventral edges are also coarsely serrated. The subocular shelf is confined to the second infraorbital. All these features are typical of trachichthyids. There is no trace of an antorbital.

Palate and jaws. The hyomandibular is inclined posteriorly a little but the quadrate and the elongated symplectic are inclined forwards so that the articular condyle of the quadrate lies only just behind the centre of the orbit, and the gape is shorter than in most trachichthyids. The endopterygoid is toothless, as usual in Berycoidei. There is a long patch of teeth on the border of the anterior part of the palate, but whether these teeth extend on to the ectopterygoid or are all on the palatine cannot be seen. There is a normal maxillary process on the tip of the palatine.

The upper jaw (Text-fig. 5, Pl. 2, fig. 2) is remarkable in having a long, toothed maxilla which makes up more than half of the gape. The premaxilla is not well preserved in either specimen and the details of the head of the bone cannot be made out, but the ascending process was clearly very small, no higher than and probably hardly distinct from the articular process. The alveolar process, extending back below the maxilla, bears minute clustered teeth on its ventro-medial surface and a single irregular row of six or seven long, slender teeth along its outer margin. On the dorsal surface of the alveolar process there is a low, rounded postmaxillary process lying medial to the maxilla. The total length of the premaxilla is about 40% of the length of the maxilla. As in the premaxilla, the articular head of the maxilla is not well preserved. Above the alveolar process of the premaxilla the maxilla extends back as a stout rod which deepens abruptly at the hind end of this process ; along the margin of this deep posterior part of the maxilla there is a single irregular series of about a dozen long, slender teeth, the anterior ones curved forwards. The anterior end of the toothed border of the maxilla projects forwards medial to the tip of the premaxilla in exactly the same way as in the ctenothrissiform *Aulolepis*
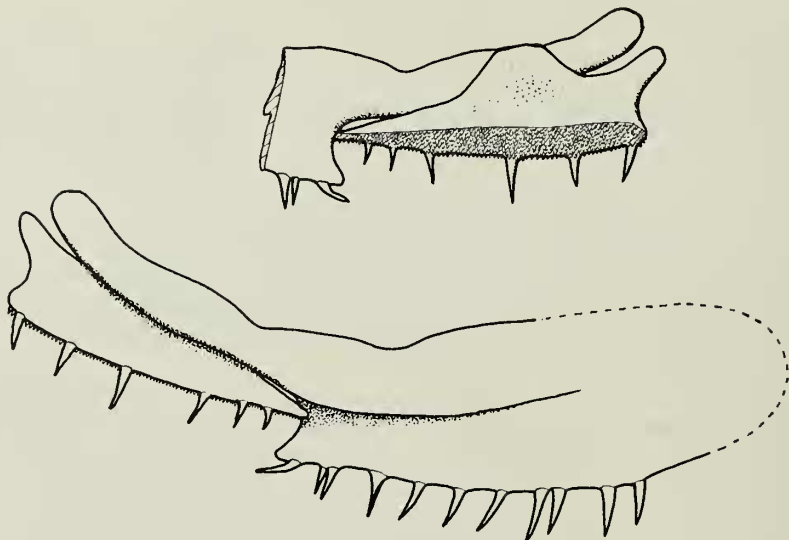
FIG. 5.   *Gnathoberyx stigmosus* gen. et sp. nov.   Left upper jaw.   Below, in lateral view ;
above, the anterior part of the jaw in medial view.   ×12 approx.

(Text-fig. 6B).   On the outer face of the toothed part of the maxilla there is a groove, overhung by a flange anteriorly, which closely resembles the groove in *Ctenothrissa* which I (Patterson, 1964 : 232 ; Text-fig. 6A) interpreted as housing a ligament attaching the upper jaw to the mandible.   The hind end of the maxilla is not completely preserved in either specimen : the bone evidently became much thinner and was without teeth.   The dorsal edge of the toothed part of the maxilla is thin and smooth so far as it is preserved, and in neither specimen is there any trace of supra-maxillae : if these were present they must have been small and flimsy, not like the large supramaxillae of Ctenothrissiformes and most Berycoidei.   In contrast to most of the superficial bones of the head, the upper jaw is smooth and without ornament.

The head of the quadrate lies almost below the centre of the orbit, and the mandible is rather short.   The ventral edge of the dentary and the flange overhanging the groove for the sensory canal on both the dentary and articular are produced into large, closely packed, recurved spines.   In size and shape these spines resemble the large marginal teeth of the upper jaw, but differ from them in having no pulp cavity. The oral border of the dentary bears small, clustered teeth, apparently with a single large procumbent tooth at the symphysis.   Whether the mandibular sensory canal ran in a closed tube or in an open groove cannot be seen.

Opercular bones.   The preopercular is typically trachichthyid, but because of the forward position of the suspensorium the ventral limb is about half as long as the dorsal and the angle in the bone is acute, almost 90°.   The bone is broad throughout its length and, as usual in Cretaceous trachichthyids, without a spine at the angle.

At and below the angle in the bone there are three stout ridges ending in marginal spines, with similar spines spaced out between them, and above the angle there are several shorter radiating ridges.

The opercular is without scales (except perhaps at its antero-dorsal corner, which is not visible) and has a series of stout, spiny ridges radiating from its point of suspension and ending in spines on the edge of the bone.   The subopercular bears similar spiny ridges radiating from its antero-dorsal corner, and on the elongated interopercular there are rows of spines radiating from the centre of the bone.

Hyoid arch and branchiostegals.   No details of the hyoid skeleton are visible in either specimen.   There are eight branchiostegal rays, the first three with coarse spines along their ventral edges.

Vertebral column.   There are eleven abdominal vertebrae and sixteen caudals, including a free second ural centrum.   The ribs are small and intermuscular-like on the first three abdominal vertebrae and are borne on transverse processes on the last three.   There are no epineurals and no epipleurals are visible.   The caudal skeleton is preserved only in the holotype ; although it is compressed and distorted it appears to agree with that of the living trachichthyid *Hoplostethus* (Gosline, 1961 : 14) in having no neural spine on the second pre-ural centrum, a slender urodermal " wedged into " the first pre-ural centrum and a separate second ural centrum, which appears larger than that of *Hoplostethus*.

Pectoral and pelvic girdles and fins.   There is a broad extrascapular of the usual triradiate form and a forked suprascapular with a long dorsal limb and a few spines near its postero-dorsal corner.   The supracleithrum is not clearly visible in either specimen.   The posterior plate of the cleithrum bears a few spiny ridges and small spines near its posterior edge.   Both the endoskeletal pectoral girdle and the pectoral fin are poorly preserved in the holotype, and in 103838 they are missing.   The anterior process of the coracoid appears to have been short and slender, meeting the cleithrum well above its tip.   The ventral postcleithrum reaches the ventral border of the trunk just behind the origin of the pelvic fin and the pelvic girdle probably made contact with the cleithrum.   The pelvic girdle and fin are missing in 103838 and in the holotype only the spine of the pelvic fin is visible ; it is ridged and equal in length to about one-third of the depth of the trunk.

Median fins.   The dorsal fin contains four stout spines, strongly ridged and increasing in length from front to rear, and nine soft rays.   The fourth dorsal spine is equal in length to about 55% of the maximum depth of the trunk.   The first dorsal radial lies between the third and fourth neural spines and is preceded by three predorsals, one in front of each of the first three neural spines.   Except for the first two and last three dorsal radials (two to each vertebra) there is a one-to-one relationship between the fin supports and the vertebrae.

The anal fin contains four stout, ridged spines and eight soft rays.   The fourth anal spine is equal in length to about half the depth of the trunk.   The first anal radial is enlarged but not hooked forwards distally.   The last anal radial lies in front of the fifth haemal spine.

The caudal fin is almost entirely missing in 103838.   In the holotype only the upper lobe of the fin is preserved.   This contains three small spines, one short

segmented ray and ten principal rays, the outermost unbranched. The presence of nine branched rays in the upper lobe is normal in caudal fins with seventeen branched rays.

Squamation. The body scales are thin but coarsely ctenoid and spiny, with their exposed surfaces covered with small spines. The lateral line scales are enlarged and thickened, each with a raised, ornamented bridge covering the sensory canal. There is a series of enlarged, thickened and coarsely ornamented ridge scales along the ventral border of the trunk in front of the anal fin, with a pair of enlarged, thickened and ornamented axillary scales at the origin of the pelvic fins. The dorsal ridge scales in front of the dorsal fin also appear to be slightly thickened. The scales do not cover the median fins but form a sheath along their bases, as in *Trachichthys*. The scales cannot be counted exactly, but they were clearly larger below the enlarged lateral line scales. There were about thirteen scales in each transverse series, with about six below and above the lateral line. Scales cover the cheek.

AFFINITIES. *Gnathoberyx* is shown to be a member of the sub-order Berycoidei by the presence of fin spines, a pelvic spine, eight branchiostegal rays, a caudal skeleton with a free second ural centrum and a caudal fin with seventeen branched rays. Within the Berycoidei the genus falls in the Trachichthyidae because of the form of the skull roof, the deep infraorbitals with a subocular shelf only on the second, the broad, cavernous preopercular, the short dorsal and anal fins, and the enlarged lateral line scales and ventral ridge scales.

The species shows various resemblances to other trachichthyids, living and fossil, such as the spiny head bones and scales (cf. *Hoplopteryx spinulosus*, also from Sahel Alma), the enlarged lateral line scales (cf. *Tubantia* from the Campanian of Westphalia and the living genera *Gephyroberyx* and *Hoplostethus*), and the short dorsal and anal fins, with four spines and less than ten soft rays (cf. *Tubantia* and *Lissoberyx* among Cretaceous forms). But the structure of the upper jaw, with a long, toothed maxilla apparently without supramaxillae, clearly sets the species apart from all other berycoids and makes a new genus necessary to receive it. The upper jaw of *Gnathoberyx*, improbable as it is in a genuine acanthopterygian, is not entirely out of place in the Berycoidei, for maxillary teeth are already known in the living *Myripristis* and the Cretaceous *Hoplopteryx macracanthus* (Patterson, 1964 : 439 ; Text-fig. 6E, F). In these forms, however, the maxilla hardly enters the gape, forming less than a quarter of the margin of the jaw. In *Gnathoberyx* the maxilla is the dominant bone in the upper jaw, in typical clupeiform or protacanthopterygian (Greenwood, Rosen, Weitzman & Myers, 1966) fashion. In particular there are striking resemblances to the upper jaw of the Ctenothrissiformes *Aulolepis* and *Ctenothrissa* (Text-fig. 6A, B), and also to the upper jaw in the living *Macristium* (Text-fig. 6C) which Marshall (1961) has suggested is a living ctenothrissoid, a hypothesis which I earlier (Patterson, 1964 : 243) felt to be unproven. The similarities between the upper jaws of *Gnathoberyx* and *Macristium* extend to the form of the premaxillary teeth and the apparent absence of supramaxillae. Without more material of *Gnathoberyx* it is impossible to study the articular heads of the premaxilla and maxilla to discover whether these resemblances are more than superficial, but in view
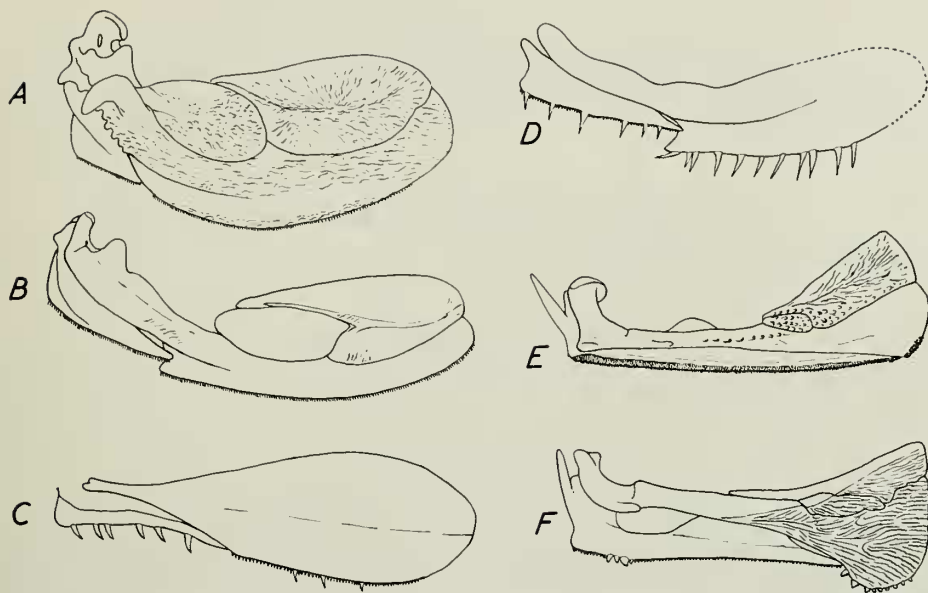
Fig. 6. The left upper jaw in lateral view of Ctenothrissiformes (left) and Berycoidei (right). *A. Ctenothrissa radians* (Agassiz), Ctenothrissidae, Upper Cenomanian, S.E. England, ×1·5. *B. Aulolepis typus* Agassiz, Aulolepidae, Upper Cenomanian, S.E. England, ×2. *C. Macristium chavesi* Tate Regan, Macristiidae (? Ctenothrissiformes), Extant, Atlantic, ×27. After Marshall, 1961. *D. Gnathoberyx stigmosus* gen. et sp. nov., Trachichthyidae, Upper Senonian, Sahel Alma, Lebanon, ×8. *E. Hoplopteryx macracanthus* Patterson, Trachichthyidae, Senonian, S.E. England, ×1·5. *F. Myripristis murdjan* Forskael, Holocentridae, Extant, Red Sea, ×1·6.

of the evidence that the Ctenothrissiformes lie closer than any other group to the ancestry of the Beryciformes (Patterson, 1964 : 463–466 ; Greenwood *et al.*, 1966 : 369) they must be carefully considered. There can be little doubt that the maxillary dentition of *Gnathoberyx* is primitive, not secondary. In *Hoplopteryx macracanthus* and *Myripristis* there is every reason to believe that this is true (Patterson, 1964 : 440), and the argument receives added force from the well-toothed maxilla of *Gnathoberyx*. But it is possible that the upper jaw of *Gnathoberyx* is specialized, for whatever purpose, by reduction in the ascending process of the premaxilla and elongation of the toothed part of the maxilla, secondarily producing a ctenothrissiform type of jaw from a more typical berycoid one. Some support for this hypothesis may be found in the relatively late age of *Gnathoberyx* (U. Senonian compared with the first trachichthyids in the L. Cenomanian) and in the generally specialized aspect of the fish—abundant spiny ornament, enlarged lateral line and ventral ridge scales, the short gape, reduced or lost supramaxillae and large marginal teeth in the upper jaw. And in one respect, the presence of a well developed postmaxillary process on the premaxilla, the upper jaw of *Gnathoberyx* is clearly advanced over those of the Ctenothrissiformes and resembles normal acanthopterygians. These facts suggest

that the resemblance between the upper jaws of *Gnathoberyx* and the Ctenothrissiformes is not necessarily evidence of close relationship, but this resemblance certainly adds to the evidence supporting the hypothesis that the Beryciformes evolved from near the Ctenothrissiformes rather than from the myctophoids, in which the maxilla is never toothed.

Family **HOLOCENTRIDAE** Richardson 1846

DIAGNOSIS.   See Patterson (1964 : 341).

Subfamily **CAPROBERYCINAE** nov.

DIAGNOSIS.   See p. 97.

Genus *STICHOCENTRUS* nov.

DIAGNOSIS.   Cretaceous Holocentridae with a moderately high supraoccipital crest projecting above the skull roof, frontals covering the anterior part of the parietals, small mucus cavities on the skull roof ; nasals small and tubular ; no antorbital, infraorbitals moderately deep, lachrymal large and deep, not extending back below the first infraorbital, no subocular shelf on first infraorbital ; superficial bones of the head (except the maxilla) ornamented with ridges, spines and tubercles ; head of hyomandibular broad and single, suspensorium inclined backwards a little, ectopterygoid toothed, no maxillary teeth ; no spine on the preopercular ; 26 vertebrae, no free ural centrum ; nine dorsal spines, the last four decreasing in length a little but dorsal fin not divided, five anal spines, the fourth thicker than the fifth but a little shorter ; scales large, rough and ctenoid, abdominal ridge scales present.

TYPE SPECIES.   *Stichocentrus liratus* sp. nov.

Stichocentrus liratus sp. nov.
(Pl. 3 ; Text-figs. 7–9)

DIAGNOSIS.   As for genus, only species.   Reaching about 7 cm. in standard length ; D IX, 11 ; A V, 9 ; P. 11 ; V I, 7.

HOLOTYPE.   B.M. (N.H.) No. P.47835 (Pl. 3).

MATERIAL.   In addition to the holotype, seven specimens in the Day Colln., American University, Beirut, AUB 105736, 105987, 106809, 108923–24, 108927, 108929.

HORIZON AND LOCALITY.   Middle Cenomanian ; Hajula, Lebanon.

DESCRIPTION.   The description and figures are based mainly on the holotype and AUB 108924 which have been prepared with acid after embedding in resin.

Measurements and proportions.   The dimensions of the more complete specimens are given in Table 2.

TABLE 2.—Dimensions (in mm.) of the five most complete specimens of
Stichocentrus liratus gen. et sp. nov.

Specimen	Total length	Standard length	Maximum depth	Length of head	Predorsal length	Preanal length
P.47835	76	64	32	30	29	54
AUB 105736	56	44	—	22	20	37
,, 105987	50	42	19	19	19	—
,, 106809	—	c.74	—	c.35	—	c.57
,, 108929	c.41	c.34	c.17	c.15	—	c.25
mean % standard length	121%	100%	48%	46·5%	45%	78%

Stichocentrus liratus was a small, moderately deep-bodied fish of normal berycoid form (Text-fig. 9). The largest specimen, AUB 106809, is very incomplete but must have had a standard length of about 74 mm. : this would give a total length of about 90 mm. The length of the head and the maximum depth of the trunk are approximately equal, about 47% of the standard length.

Neurocranium. The neurocranium is typically holocentrid in shape, broad and deep posteriorly and tapering forwards. The skull roof (Text-fig. 7) is well exposed in the holotype and 108924. There was a moderately large supraoccipital crest (*soc.*) with a thickened anterior edge ; the crest is higher and longer than it is in living holocentrids, but not so large as it is in *Caproberyx* (Patterson, 1964, text-fig. 67 ; Text-fig. 10). The supraoccipital crest arises from a short, broad, shallow supratemporal fossa (*st. f.*), limited anteriorly by the frontals and parietals. Again, the fossa is larger than it is in living holocentrids but smaller than in *Caproberyx*. The parietals (*pa.*) are separated by the supraoccipital and bear a raised area, ornamented with ridges and tubercles ; the parietal branch of the supraorbital sensory canal opened through a pore in the frontal immediately in front of this area, and passed into a depression on the parietal from which two short grooves, the medial one bifurcated, lead on to the ornamented area. The parietals bear very similar grooves and depressions in the living holocentrid *Holotrachys*. The supratemporal articulated with the hind edge of this ornamented area, transmitting the terminal part of the supratemporal commissural sensory canal, which ran in a short groove behind the ornamented area. It is possible that the parietal met the pterotic in the wall of the post-temporal fossa (*pt. f.*), but the area where the two bones would have made contact is covered by a posterior extension of the frontal. The ventral limb of the supratemporal articulated with the pterotic (*pto.*), and the main cephalic sensory canal passed forwards in a groove covered laterally by a smooth raised flange on this bone. The preopercular sensory canal passed ventrally through a notch at the hind end of this flange. The sphenotic (*spo.*) has the dermal and cartilage components completely fused. The infraorbital sensory canal passed ventrally between two raised, ornamented flanges on the sphenotic.

The frontals (*fr.*) are very large, extending posteriorly to cover much of the parietals and pterotics, a characteristic holocentrid feature. In *Stichocentrus* this posterior extension of the frontals is not so marked as it is in living holocentrids but
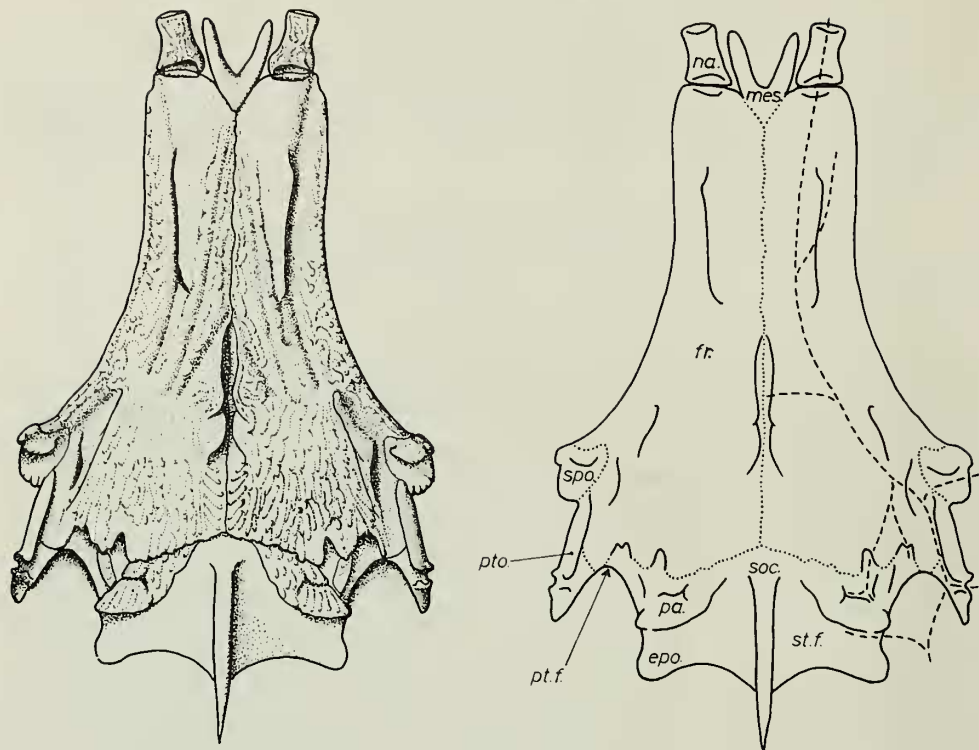
FIG. 7.   *Stichocentrus liratus* gen. et sp. nov.   Restoration of the skull roof in dorsal view,
×5 approx.   *epo.*, epiotic ; *fr.*, frontal ; *mes.*, mesethmoid ; *na.*, nasal ; *pa.*, parietal ;
pt.f., post-temporal fossa ; *pto.*, pterotic ; *soc.*, supraoccipital ; *spo.*, sphenotic ; *st.f.*,
supratemporal fossa.   The broken line on the right side of the key diagram shows the
course of the sensory canals.

greater than it is in *Caproberyx*.   Most of the surface of the frontal, particularly the
posterior part and the supraorbital flange, is strongly ornamented with small
tubercles and sinuous ridges : this ornament resembles that in *Caproberyx superbus*
rather than the large straight ridges on the frontals of living holocentrids.   The
supraorbital sensory canal passed on to the frontal from the sphenotic, gave off a
short branch into a depression on the posterior part of the supraorbital flange, and
then entered the bone through an elongated pore.   Within the bone the canal gave
off two posterior branches which passed back in tubes to the hind end of the frontal,
the more medial of these branches leading into the depression and grooves on the
parietal.   The sensory canal gave off a medial branch opening into a narrow median
channel between the frontals, similar in size and position to the median mucus cavity
in *Caproberyx superbus*, but partially roofed by raised flanges of bone.   Passing
forwards within the frontal, the sensory canal gave off a lateral branch through a
much elongated pore, covered above by a flange of bone, leading to a groove above
the anterior part of the orbit.   From a pore in the anterior end of the frontal the

canal passed into the nasal. The nasals (*na.*), which were attached to the frontals by connective tissue, not by suture, are small, tubular bones, ornamented with ridges and tubercles. Between the nasals the large " V "-shaped dorsal part of the mesethmoid (*mes.*) is exposed. There is no trace of an antorbital in any specimen : the bone was probably absent, as it is in *Caproberyx*. In the roof of the orbit of the holotype and 105736 an orbitosphenoid (*ors.*, Text-fig. 8) is visible, similar in size and shape to that of *Caproberyx superbus* but apparently without the lateral fenestra present in the latter ; in living holocentrids the orbitosphenoid is much reduced in comparison with these Cretaceous forms. As is usual in these small, crushed fishes from the Lebanon, no details of the basicranium are visible in any specimen. The parasphenoid is straight, with lateral flanges articulating with the endopterygoids. The vomer is not visible in any specimen. The lateral ethmoids (*l. e.*) are deep and well ossified.

Infraorbital series. The infraorbital series consists of the usual five bones. The two posterior infraorbitals are small and slender with coarsely serrated posterior edges and a smooth flange covering the groove for the sensory canal. The first and second infraorbitals are longer and a little deeper, with the edge of the flange over the sensory canal serrated and coarse ridges on the ventral part of the bone. There is a
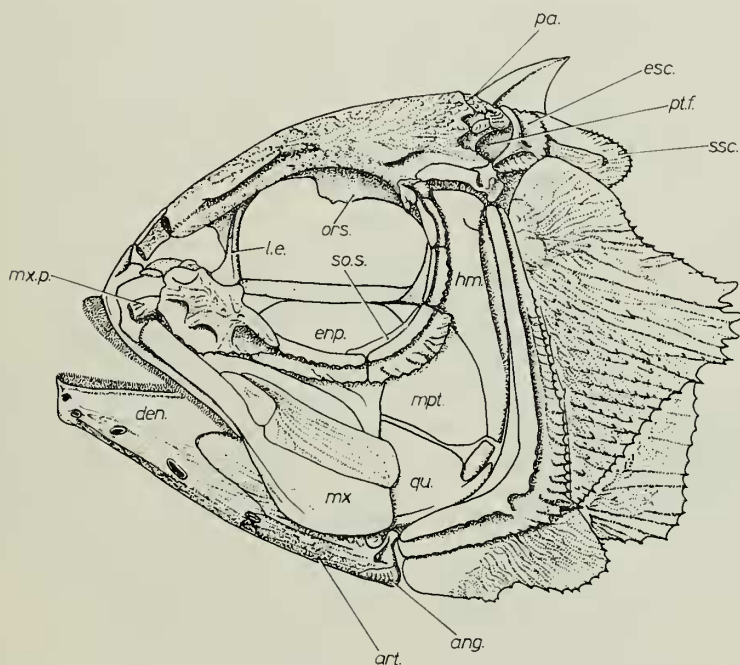
Fig. 8. *Stichocentrus liratus* gen. et sp. nov. Restoration of the skull in left lateral view, ×3·5 approx. *ang.*, angular ; *art.*, articular ; *den.*, dentary ; *enp.*, endopterygoid ; *esc.*, extrascapular ; *hm.*, hyomandibular ; *l.e.*, lateral ethmoid ; *mpt.*, metapterygoid ; *mx.*, maxilla ; *mx.p.*, maxillary process of palatine ; *ors.*, orbitosphenoid ; *pa.*, parietal ; *pt.f.*, post-temporal fossa ; *qu.*, quadrate ; *so.s.*, subocular shelf ; *ssc.*, suprascapular.

subocular shelf (*so. s.*) on the second, third and fourth infraorbitals, but not apparently on the first, although the shelf on the second infraorbital extends forwards some way along the medial face of the first. The lachrymal is deeper than the infraorbitals but does not extend back below the first infraorbital as it does in *Caproberyx* (Text-fig. 10). The groove for the sensory canal on the lachrymal is covered for most of its length by a broad bridge of ornamented bone, with two large pores in its ventral part. Dorsally the lachrymal articulated with the lateral ethmoid by a broad facet. As noted above, there is no antorbital.

Palate and jaws. The hyomandibular (*hm.*) has a broad, undivided head, and is inclined backwards a little. The symplectic inclines forwards at about 35° to the hyomandibular so that the condyle of the quadrate (*qu.*) lies below the posterior part of the orbit. The ectopterygoid and palatine are toothed but the endopterygoid (*enp.*) is toothless. The large maxillary process of the palatine (*mx. p.*) fits in a broad groove on the dorsal surface of the maxilla.

The premaxilla has a low ascending process, which is only a little over a quarter of the length of the toothed alveolar process and is hardly longer than the articular process of the bone. The toothed border of the premaxilla becomes broader and projects a little anteriorly, but the anterior teeth are not enlarged as they are in *Holocentrus* and *Myripristis*. The maxilla (*mx.*) is more than two-thirds as long again as the premaxilla and is expanded behind the latter, but is without teeth. The posterior expansion of the maxilla has a few weak ridges near the ventral margin. There are two supramaxillae, the posterior with a process overlapping the anterior. The posterior supramaxilla is strongly ornamented with longitudinal ridges. The anterior supramaxilla is rather large, extending forwards well beyond the tip of the process on the posterior bone, and is ornamented with a few very weak ridges.

The mandible is long, and moderately deep. The coronoid process of the dentary bears teeth to its tip ; the band of teeth does not become much broader at the symphysis and the teeth are not enlarged there. The ventral parts of the dentary (*den.*) and articular (*art.*) are ornamented with strong longitudinal ridges. There is a small angular (*ang.*) at the back of the jaw. The mandibular sensory canal ran in a tube, closed in the articular but with five pores in the dentary, two at the symphysis, two equally spaced along the bone, and one at the suture with the articular.

Opercular bones. The preopercular is long and strongly angulated, with its vertical limb inclined backwards a little. The posterior edge of the bone bears ridges ending in serrations which grow stronger towards the angle, where one is enlarged into a small spine. The edge of the flange covering the groove for the sensory canal is smooth except near the angle, where there are a few weak, blunt serrations and a single narrow bridge over the groove.

The opercular is large and strongly ornamented. Radiating from the point of suspension of the bone there are sinuous, bifurcating ridges and on the ventral two-thirds of the bone there is also a series of strong, parallel, spiny ridges, each ending in a coarse serration on the edge of the bone. Opposite the point of suspension there are five or six spines on the edge of the bone, with weaker serrations above them. The ornament of the opercular is very like that in *Hoplopteryx simus*, a trachichthyid from the English Chalk (Smith Woodward, 1902, pl. 8, fig. 2). On

the antero-dorsal corner of the opercular there are two or three small scales. The ornament of the subopercular is similar, with parallel ridges ending in serrations, interspersed with weaker, sinuous ridges. The large interopercular has coarse, sinuous ridges on the ventral two-thirds of its surface, and serrations on its ventral edge. In the centre of the edge of the interopercular there is an excavation : a similar excavation occurs in the living *Holocentrus*, but there it is covered by the much enlarged preopercular spine.

Hyoid arch and branchiostegals.   The ceratohyal is very deep and is perforated by a large, oval fenestra : it resembles that of *Caproberyx* (Patterson, 1964, text-fig. 73) rather than the shallow, unperforated ceratohyals of living holocentrids.   There are eight branchiostegals, the four anterior rays articulating with the medial face of the ceratohyal, the four posterior ones with the lateral face of the bone.   There is a large, rectangular urohyal.

Vertebral column.   There are 26 vertebrae, eleven abdominal and fifteen caudal. All the abdominal vertebrae except the first bear ribs, which are inserted on transverse processes on the last three.   There appear to be no epipleurals.   The caudal skeleton will be described in detail in a forthcoming work, but it agrees with that of *Holocentrus* (Gosline, 1961 : 14) in having a neural crest on the second pre-ural centrum and the second ural centrum fused with the fused first pre-ural and ural centra, although the line of fusion is clearly visible and the caudal skeleton appears more " upturned " than in living holocentrids.   The neural and haemal spines of the first three pre-ural vertebrae are expanded, as they are in living holocentrids.

Pectoral and pelvic girdles and fins.   The pectoral girdle contains the normal berycoid complement of bones.   The extrascapular (*esc.*) has serrations on its
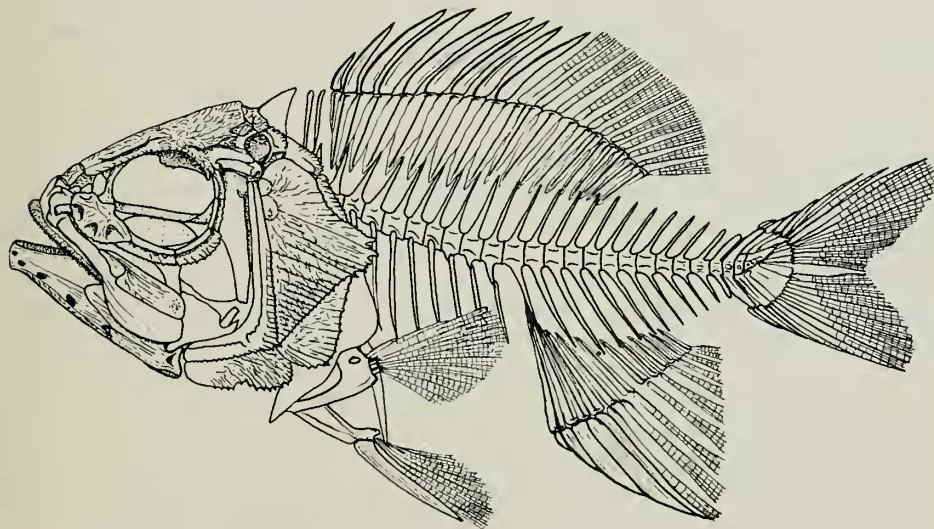

Fig. 9.   *Stichocentrus liratus* gen. et sp. nov.   Restoration of the skeleton, scales omitted, × 1·7 approx.

posterior edge, ridges ending in serrations on its ventral edge, and a ridge over the groove for the sensory canal in the centre of the bone.   On the suprascapular (*ssc.*) the sensory canal ran forwards in a groove covered by a vertical flange of bone ; this flange is ornamented with ridges, and on the edges of the posterior half of the bone there are ridges ending in serrations.   The supracleithrum bears similar ridges and serrations.   The posterior plate of the cleithrum bears only a few sinuous ridges. The anterior process of the coracoid is long and stout, arching forwards to the tip of the cleithrum.   The four pectoral radials are the usual small, hourglass-shaped bones, increasing in size downwards.   The large pectoral fin contains ten rays, the third of which is the longest.

The pelvic fins are thoracic, the pelvic bones making contact with the cleithra and the fins being inserted well in front of the tip of the ventral postcleithrum.   The pelvic fin contains a very stout, ridged spine, equal in length to the longest anal spine, and seven soft rays.

Median fins.   The dorsal fin arises close behind the head, in advance of the pectorals, and occupies most of the back of the fish.   The fin contains nine spines and eleven soft rays ; the spines are stout, gently curved, and almost smooth.   The first four spines increase in length, the fifth and sixth are equal in length and the last three decrease in length very slightly.   The spines are alternately inclined to right and left, as they are in living holocentrids, so that in the fossils they appear to be alternately thick and thin (Pl. 3).   In the holotype (64 mm. standard length), on which Text-fig. 9 is mainly based, the longest dorsal spines are equal in length to a little less than the distance between the base of the spines and the vertebral column, but in some of the smaller specimens, particularly 105987 (42 mm. standard length), the spines are longer, equal in length to about half the maximum depth of the trunk. The available material suggests that this difference is not taxonomically significant, but that the length of the dorsal spines was variable in the species and that during ontogeny the depth of the trunk increased in proportion to the length of the dorsal spines.

The first radial of the dorsal fin is not enlarged, and is inserted between the second and third neural spines.   The fin is preceded by two predorsals lying between the first and second neural spines.   The spine-bearing dorsal radials are expanded, meeting each other in slightly dentate sutures.

The anal fin originates below the middle of the soft dorsal and contains five spines, the first of which is extremely small, and nine soft rays.   The spines increase in length from front to rear and are weakly ridged and very stout.   The fifth spine, although longer than the fourth, is more slender, as in *Myripristis* (where there are only four spines).   The longest anal spine is rather variable in length : it is longer than the longest dorsal spine in the holotype, about equal to the longest dorsal spine in 105736 and 108929, and shorter than the longest dorsal spine in 108923.   The first anal radial is not much enlarged.

The forked caudal fin contains nineteen principal rays with seventeen branched (nine in the upper lobe, eight in the lower).   The principal rays are preceded by four small spines and one segmented ray above and below.

Squamation.   The scales are thick, large and coarsely ctenoid.   The exposed area

of each scale is ornamented with weak ridges and tubercles passing back to the ctenii on the hind edge. There are twelve scales in a transverse series on the trunk, with the lateral line passing through the fifth scale from the top, and about twenty-six scales along the lateral line. Scales cover the cheek and there are one or two scales on the antero-dorsal corner of the opercular. The scales overlap the bases of the dorsal and anal fins, both soft and spinous portions, as they do in living holocentrids. Between the pelvic and anal fins there is a median series of ridge scales, not enlarged or much thickened, as in *Caproberyx*.

AFFINITIES. As has been emphasized in the comparisons made in the description above, *Stichocentrus* is a holocentrid berycoid. Falling in the suborder Berycoidei because of its toothless endopterygoid, pelvic spine and nineteen-rayed caudal, it is allied with the Holocentridae rather than the Trachichthyidae by the nine dorsal spines (no more than eight in any trachichthyid), the seven soft rays in the pelvics, the absence of crests and large mucus cavities on the skull roof, the posterior extension of the frontals and the small supratemporal fossa, the large mesethmoid, the rather shallow infraorbitals with a subocular shelf on the last three, and the enlarged penultimate anal spine.

Three other genera of Cretaceous holocentrids are known : *Caproberyx* (Lower Cenomanian of Morocco, Middle Cenomanian of Hakel (p. 98) and Turonian of England), *Trachichthyoides* (Upper Cenomanian of England) and *Kansius* (Lower Senonian of Kansas). *Trachichthyoides* is known only by a single head (Smith Woodward, 1902, pl. 8, fig. 5 ; Patterson, 1964 : 359). It differs from *Stichocentrus* in having the mucus cavities on the skull roof larger and the ornamented areas and supraoccipital crest smaller, in the deeper, more strongly ornamented infraorbitals, with the lachrymal extending back below the first infraorbital, and in the shorter jaws, with the suspensorium inclined forwards. But the general features of the two skull roofs and the form and ornament of the opercular bones are very similar and in *Trachichthyoides* there is no subocular shelf on the first infraorbital, just as in *Stichocentrus*.

From *Kansius*, in which only the trunk is known (Hussakof, 1929), *Stichocentrus* differs in having one or two fewer dorsal fin spines, with a less marked decrease in length in the posterior spines, and in having the last anal spine longer than the penultimate. But in size, in the proportions of the trunk and the size and position of the fins the two genera are very similar.

In *Caproberyx* (Patterson, 1964 : 341, 416 ; p. 98) the skull roof resembles that of *Stichocentrus* more closely than any other known form, but in *Stichocentrus* the supraoccipital crest and supratemporal fossa are smaller and the frontals extend back farther. *Caproberyx* also differs from *Stichocentrus* in having only six or seven dorsal fin spines, with the last the longest, in having more soft rays in the anal fin, in the posterior extension of the lachrymal below the first infraorbital, the subocular shelf on the first infraorbital, the shorter, more strongly expanded maxilla, etc., but again there are many similarities between the two genera.

The five anal spines of *Stichocentrus* are a peculiar feature. No living holocentrid has more than four, and although five spines have been described in *Kansius*

(Hussakof, 1929 : 3) Conrad (1941 : 17) has given reasons for doubting that there were more than four, an interpretation which seems to be confirmed by Hussakof's description of the enlarged third spine as having two spines behind it, a feature known in no other holocentrid.   In *Caproberyx superbus*, which has been described as having only four spines (Smith Woodward, 1902 : 12 ; Patterson, 1964 : 357) a complete series of spines is not well preserved in any specimen, but some individuals, particularly in P.9153, appear to have had a very small anterior spine making a total of five, as in *Stichocentrus*.

Recent workers (Conrad, 1941 ; Nelson, 1955 ; Dunkle & Olsen, 1959) recognize two subfamilies in the Tertiary and recent holocentrids, the Holocentrinae, containing among living genera *Holocentrus* and *Plectrypops* according to Conrad (1941), *Holocentrus* alone according to Nelson (1955), and the Myripristinae, containing *Myripristis*, *Ostichthys*, *Holotrachys*, *Plectrypops* and *Corniger* according to Nelson (1955).   These subfamilies are differentiated by characters such as the form of the otic bulla, the spine on the preopercular, the elongated nasals and premaxillary ascending processes, short jaws and deep spiny lachrymal of *Holocentrus*.   Among Cretaceous holocentrids, *Trachichthyoides* is allied to the myripristine line in characters of the skull roof, lachrymal and preopercular, while *Caproberyx* resembles the holocentrines in the skull roof and the deep lachrymal.   *Kansius* is insufficiently known to be confidently placed in either subfamily.   *Stichocentrus* resembles *Caproberyx* and the holocentrines in its skull roof and infraorbitals, but is closer than *Caproberyx* to the living holocentrids in the nine dorsal fin spines, alternately inclined to left and right and with the last four decreasing in length, and in the enlarged penultimate anal spine.   Thus among the four known genera of Cretaceous holocentrids one can see the gradual acquisition of such Recent holocentrid features as the form of the dorsal and anal fins (in the sequence *Caproberyx–Stichocentrus–Kansius*), the posterior extension of the frontals and the reduction of the supratemporal fossa and supraoccipital crest (in the sequence *Caproberyx–Stichocentrus*), the development of a subocular shelf on all the infraorbitals (in the sequence *Trachichthyoides–Stichocentrus–Caproberyx*).   But all these Cretaceous genera (so far as they are known) differ from the Tertiary and living holocentrids in a number of characters such as the absence of an antorbital, the simple, tubular nasals, the large pores along the course of the mandibular sensory canal (in living holocentrids the mandibular sensory canal is almost entirely enclosed), the presence of scales only on the antero-dorsal corner of the opercular (in living holocentrids scales cover the whole anterior part of the opercular), the deep, perforate ceratohyal and the occasional presence of five anal spines.   Some of these characters are certainly primitive, but others such as the absence of an antorbital and maxillary teeth and the five anal spines are specialized and seem to exclude the known Cretaceous holocentrids from the direct ancestry of later members of the family.   Certainly the Cretaceous holocentrids are more closely related to each other than they are to the Tertiary and living genera, and they cannot reasonably be included in either of the subfamilies recognized among living forms (these subfamilies seem merely to emphasize the specializations of *Holocentrus* itself).   At present the evidence suggests that the Holocentridae underwent two radiations, one in the Cretaceous and one in the Tertiary, the Tertiary forms

being derived from ancestors as yet unknown.   In the Cretaceous radiation the fins and skull roof gradually acquired features approaching those of modern forms, but there remain considerable differences between the two groups.   I propose that the Cretaceous forms be included in a new subfamily Caproberycinae, defined as follows : Holocentridae in which the dorsal fin is undivided, with 6–11 spines, anal with 4–5 spines, the penultimate sometimes enlarged, nasals simple and tubular, no antorbital, no maxillary teeth, large pores along the course of the mandibular sensory canal, otic bulla as in *Myripristis* where known, no preopercular spine, only two or three scales on the antero-dorsal corner of the opercular, ceratohyal deep and perforate.

One other species must be mentioned in discussing *Stichocentrus*.   This is *Hoplopteryx lewisi* (Davis), under which name the specimens of *Stichocentrus* in Beirut were catalogued by Smith Woodward (in *ms.*).   *Stichocentrus liratus* and *Hoplopteryx lewisi* are distinguished by the occurrence of the first only at Hajula, the second only at Hakel, and by the presence in *H. lewisi* of only 22–23 vertebrae (not 22–24 as I stated : Patterson, 1964 : 406), a long premaxilla, an unexpanded maxilla, a large supratemporal fossa extending well forward over the orbit, the penultimate anal spine not enlarged, etc.   But in size, shape and proportions of the trunk, number and structure of the fin spines and the shape and ornamentation of the superficial bones of the head the two species are strikingly similar.   Further, in P.8689 and P.10709 (*H. lewisi*) there are traces of at least one large scale on the antero-dorsal part of the opercular, a difference from all other trachichthyids except *Lissoberyx* (p. 77) and a resemblance to *Stichocentrus*.   This tends to confirm that the scaleless opercular of trachichthyids is secondarily derived from a scaly opercular (p. 107).   The strong similarity between *Stichocentrus liratus* and *Hoplopteryx lewisi* provides further evidence of the close relationship between the Holocentridae and Trachichthyidae in the Cretaceous : in the English Chalk a similar comparison may be made between *Hoplopteryx lewesiensis* and *Caproberyx superbus*, but here we know that the similarities extend to habitat as well as habitus, for in B.M. (N.H.) 33486 two large individuals, one of *C. superbus* and one of *H. lewesiensis*, are preserved side by side in the same block of Chalk.

Genus *CAPROBERYX* Tate Regan, 1911 : 8

DIAGNOSIS.   See Patterson (1964 : 341), but add " lachrymal extending back below first infraorbital, dorsal fin with six or seven spines, dorsal spines not alternately inclined to right and left, scales moderately large, about 12–15 in each transverse series ".

TYPE SPECIES.   *Beryx superbus* Dixon (1850) (= *Berycopsis major* Smith Woodward) from the Turonian zones of the English Chalk.

Caproberyx pharsus sp. nov.
(Pl. 4, fig. 2 ; Text-fig. 10)

DIAGNOSIS.   A *Caproberyx* known only by a specimen lacking the posterior half of the trunk ; probably about 6·25 cm. in standard length ; length of head slightly

less (93%) than maximum depth of trunk, the latter probably equal to about 45% of the standard length ; skull roof without ornament except for a few ridges on the parietal, the supraorbital flange and near the median mucus cavity, which is partially roofed, as in *Stichocentrus* ; infraorbitals with serrated edges, otherwise smooth, posterior infraorbitals not tubular ; hind margins of preopercular and opercular coarsely serrated, operculum with weak radiating ridges ; dorsal fin with six spines, pelvic apparently with only six soft rays ; scales thick on antero-ventral part of trunk, thin elsewhere, 15 or 16 scales in a transverse series.

HOLOTYPE.   B.M. (N.H.) P.47836 (Pl. 4, fig. 2), a fish lacking the posterior half of the trunk, part of the head in counterpart.   The only specimen.

HORIZON AND LOCALITY.   Middle Cenomanian ; Hakel, Lebanon.

DESCRIPTION.   Since this species is known only by a single incomplete and rather poorly preserved specimen the description which follows is incomplete, and the assignment to *Caproberyx* must be regarded as provisional.   The specimen has been prepared by transfer in a resin block.

Measurements and proportions.   The length of the preserved part of the fish (to the second caudal vertebra) is 40 mm. ; the standard length is estimated to have been about 6·25 cm.   The length of the head is 26 mm., the maximum depth of the trunk 28 mm.   The species was thus rather deep-bodied, the depth of the trunk being greater than the length of the head and equal to about 45% of the standard length, compared with about 40% in the other known species of *Caproberyx*.

Neurocranium.   The skull roof is shown in Text-fig. 10.   There is a high, triangular supraoccipital crest (*soc.*), thickened anteriorly, which is larger than that of *Stichocentrus* (Text-fig. 7) but smaller than in *C. superbus* (Patterson, 1964, text-fig. 67). The supratemporal fossa was clearly short and broad, as in *Stichocentrus* and *C. superbus*, but detailed comparisons are not possible.   The parietals (*pa.*) are poorly preserved, but near the mid-line they bore an area of fine ridged and tubercular ornament.   Laterally, the parietal extends ventrally in the wall of the post-temporal fossa ; while it is impossible to be certain how much of this wall was formed by the parietal it appears that there was a broad contact, not covered by the frontal, between the parietal and the pterotic (*pto.*) in the wall of the fossa.   This is a primitive feature which does not occur in *Caproberyx superbus* or *Stichocentrus*, but is present in *Trachichthyoides* and *Lissoberyx* (Text-fig. 2) and is indicated in Arambourg's figure (1954, text-fig. 68) of the skull roof of *Caproberyx polydesmus*.   The frontal appears to extend as far postero-laterally as it does in *C. superbus* but not so far as in *Stichocentrus* and in general the posterior part of the skull roof seems closest to that of *Caproberyx* but with a more complete roof to the post-temporal fossa.   The frontals (*l. fr.*, *r. fr.*) are much less strongly ornamented than they are in *Caproberyx* and *Stichocentrus*, the only ornament consisting of a few weak ridges on the flange which roofs the median mucus cavity (see below) and a series of short ridges on the supraorbital flange of the bone.

The main cephalic sensory canal, passing on to the pterotic from the extrascapular, ran forwards in an open groove, covered laterally by a raised flange, with the preopercular sensory canal passing ventrally behind this flange in the usual way.
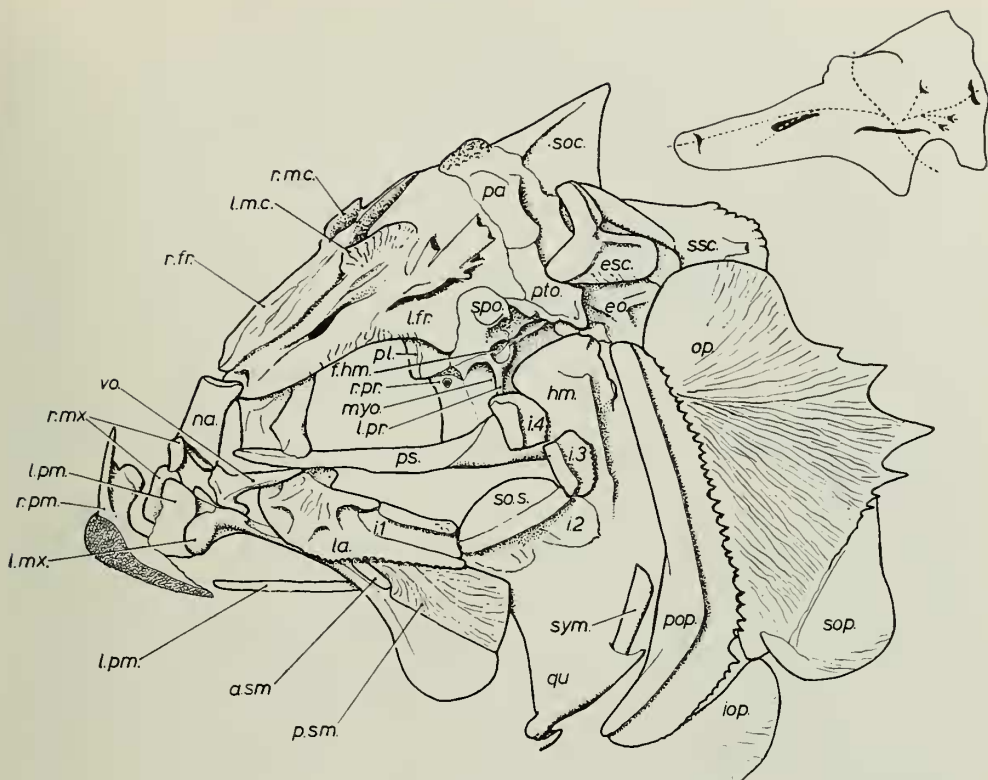
FIG. 10. *Caproberyx pharsus* sp. nov. The head of the holotype as preserved, some bones partially restored from the counterpart, ×5 approx. Inset at top right is a diagram of the left frontal showing the course of the supraorbital sensory canal. *a.sm.*, anterior supramaxilla ; *eo.*, exoccipital ; *esc.*, extrascapular ; *f.hm.*, articular facet for hyomandibular ; *hm.*, hyomandibular ; *i.1, i.2, i.3, i.4*, infraorbitals 1–4 ; *iop.*, interopercular ; *la.*, lachrymal ; *l.fr.*, left frontal ; *l.m.c.*, roof of median mucus cavity on left frontal ; *l.mx.*, left maxilla ; *l.pm.*, fragment of head and alveolar process of left premaxilla ; *l.pr.*, left prootic ; *myo.*, myodome ; *na.*, left nasal ; *op.*, opercular ; *pa.*, parietal ; *pl.*, left pleurosphenoid ; *pop.*, preopercular ; *ps.*, parasphenoid ; *p.sm.*, posterior supramaxilla ; *pto.*, pterotic ; *qu.*, quadrate ; *r.fr.*, right frontal, crushed and displaced ; *r.m.c.*, roof of median mucus cavity on right frontal ; *r.mx.*, head of right maxilla ; *r.pm.*, right premaxilla ; *r.pr.*, right prootic ; *so.s.*, subocular shelf on second infraorbital ; *soc.*, supraoccipital crest ; *sop.*, subopercular ; *spo.*, left sphenotic, its orbital margin bent upwards ; *ssc.*, suprascapular ; *sym.*, symplectic ; *vo.*, vomer.

Passing over the surface of the sphenotic (where there was presumably an anastomosis with the infraorbital canal), the supraorbital canal ran antero-dorsally on to the frontal and entered a horizontal tube in the bone through a much elongated foramen (inset, Text-fig. 10). There is no sign in *C. pharsus* of the depression on the supraorbital flange of the frontal which in *C. superbus* and *Stichocentrus* received a branch given off from the canal before it entered the bone : the great elongation in *C. pharsus*

of the foramen through which the canal entered the bone suggests that this branch was given off within the opening, approaching the condition in living holocentrids where the branch is given off after the canal has entered the tube in the bone. In the tube in the frontal the canal gave off the usual posterior branch, which in *C. pharsus* was subdivided into four (compared with two in *C. superbus* and *Stichocentrus*), one large branch passing back in a tube to the hind end of the frontal, a smaller and shorter branch in a tube above this and two still smaller and shorter ones below it (inset, Text-fig. 10). The medial branch of the supraorbital canal passed into an elongated median mucus cavity, similar in size and position to that of *C. superbus* but partially roofed by a raised, ornamented flange of bone (*l.m.c., r.m.c.*), as in *Stichocentrus* (Text-fig. 7). After giving off the median branch, the supraorbital canal passed forwards within the frontal to its anterior end, giving off a lateral branch through an elongated pore above the anterior half of the orbit.

Only the left nasal (*na.*) is preserved, a moderately large, trapezoid bone, without ornament and apparently tubular, enclosing a broad passage for the sensory canal, as in *Stichocentrus*.

The vomer (*vo.*) is preserved but displaced, and it is impossible to see whether it bore teeth. The parasphenoid (*ps.*) is straight and toothless, as is normal in holocentrids. The anterior parts of the prootics are visible (*l. pr., r. pr.*), showing nothing to distinguish them from the prootics of *C. superbus*. A wide myodome (*myo.*) opens between the prootics. The elongated facet for the hyomandibular (*f. hm.*) is formed by the prootic, sphenotic and pterotic, in the usual way, and there is a large dilatator fossa in the sphenotic and pterotic above this facet. No basisphenoid is preserved. The pleurosphenoid (*pl.*) appears to be larger than in *C. superbus* and shows the usual groove for the superficial ophthalmic nerves. Traces of an orbitosphenoid are preserved, but the shape of the bone cannot be made out.

Infraorbital series. The infraorbital series contains the usual five bones. The lachrymal (*la.*) resembles that of *Caproberyx superbus* (Patterson, 1964, text-fig. 70) in depth and in the long postero-ventral process extending back below the first infraorbital to touch the second ; as in *C. superbus* there is a broad bridge over the groove for the sensory canal, with large pores near the ventral margin, but the surface of the bone is almost smooth. The ventral edge of the lachrymal is serrated. The first infraorbital (*i.* 1) is shallow and unornamented except for a few ridges on the posterior part of the flange over the sensory canal. The second, third and fourth infraorbitals (*i.* 2–4) are all deeper than the corresponding bones in *C. superbus* and much deeper than those of *Stichocentrus* ; they have a smooth flange over the groove for the sensory canal and serrated ventral edges. The second infraorbital, incomplete ventrally, has a broad groove in its centre marking a branch of the sensory canal. There is a very broad subocular shelf (*so. s.*) on the second infraorbital, but whether the shelf was present on all the infraorbitals as in *C. superbus* and living holocentrids cannot be seen.

Palate and jaws. The hyomandibular (*hm.*) has a broad, undivided head and a very broad proximal part, as in *C. superbus*. The hyomandibular is inclined backwards a little, with the symplectic (*sym.*) and quadrate (*qu.*) inclined forwards so that the quadrate condyle lies below the posterior edge of the orbit. The endopterygoid

is toothless but the anterior part of the ectopterygoid is toothed. The palatine is not visible.

The premaxilla (*r. pm.*) has a rather high ascending process, probably equal in length to about one-third of the toothed alveolar process (although the latter is not completely preserved). As in *Stichocentrus*, the tooth patch on the premaxilla becomes broader anteriorly, but there are no enlarged teeth. The maxilla (*l. mx.*) is about 40% longer than the premaxilla, as in *C. superbus*, proportionately much shorter than in *Stichocentrus*. The maxilla is expanded behind the premaxilla and is without ornament or teeth. There are two supramaxillae, the posterior one (*p. sm.*) ornamented with ridges radiating from a longitudinal ridge in the centre of the bone, the anterior (*a. sm.*) almost smooth. The posterior supramaxilla bears the usual process overlying the anterior.

Of the mandible almost nothing is preserved. The bones were clearly only feebly ornamented.

Opercular series and branchiostegals. The preopercular (*pop.*) is bent through about 50°, compared with 60° in *C. superbus* and *Stichocentrus*. The dorsal limb of the preopercular is inclined backwards a little. The broad flange covering the groove for the sensory canal is smooth, as in *C. superbus*, and does not form a bridge at the angle in the bone as it does in *Stichocentrus*. The hind edge of the preopercular is strongly and coarsely serrated but there is no enlarged spine at the angle in the bone.

The posterior edge of the opercular (*op.*) is produced into spines, with a large one opposite the point of suspension and a larger one just below, as in *C. polydesmus* (Arambourg) but not in *C. superbus*. The ornament of the opercular, weak ridges radiating from the point of suspension, resembles that in *C. superbus* and is quite unlike that in *Stichocentrus*. There are two or three scales on the antero-dorsal corner of the opercular, as is usual in Cretaceous holocentrids. The subopercular (*sop.*) and interopercular (*iop.*) are poorly preserved but appear to have been of normal form, the interopercular with ridges near its ventral edge, the subopercular with a few ridges, possibly ending in weak serrations, at its antero-ventral margin.

The hyoid arch and branchiostegals are very imperfectly preserved : most of the branchiostegals are missing and their number cannot be estimated.

Vertebral column. Only the first thirteen vertebrae are preserved. There are eleven abdominal vertebrae, the last four with transverse processes on which the ribs are inserted. Whether there are ribs on the second centrum, as there are in *Stichocentrus* and *Lissoberyx*, cannot be seen. Epipleural bones are visible articulating with the centra of the last three abdominal vertebrae.

Pectoral and pelvic girdles and fins. The extrascapular (*esc.*) is similar in shape to that of *C. superbus*, with a short, broad ventral limb and a longer, more slender dorsal limb, but has a smooth posterior edge and only a few weak ridges on the ventral limb. The suprascapular (*ssc.*) has a moderately long dorsal limb and a very broad posterior plate, with a coarsely serrated hind margin. The supracleithrum appears to be less broad than that of *C. superbus* and has coarse serrations on the upper part of its posterior edge. The posterior plate of the cleithrum is smooth. Of the endoskeletal pectoral girdle nothing can be seen. The ventral postcleithrum reaches the ventral border of the trunk well behind the origin of the pelvic fin and the pelvic

girdle was in contact with the cleithra. The pectoral fin contains about eleven rays and is rather small, its length being only about one-quarter of the maximum depth of the trunk. The pelvic fin contains a stout, weakly ribbed spine, equal in length to a little more than one-third of the maximum depth of the trunk, and apparently only six soft rays, a difference from *C. superbus* and all other holocentrids which is possibly due only to imperfect preservation, although the fin appears to be complete.

Median fins. Of the median fins, only the anterior part of the dorsal fin is preserved. This contains six smooth spines, increasing in length from front to rear, and nine soft rays : there were probably two or three more soft rays. The spines are not alternately inclined to left and right as they are in *Stichocentrus* and living holocentrids. The longest spine, the sixth, is equal in length to about 40% of the maximum depth of the trunk. The first dorsal radial, supporting the first and second spines, is inserted between the third and fourth neural spines. Preceding the dorsal fin there are three predorsals, one lying in front of each of the first three neural spines.

Squamation. The scales on the antero-ventral part of the trunk are thick and coarsely ctenoid ; on the rest of the trunk the scales are much thinner and though their hind margins are nowhere perfectly preserved they appear to be feebly ctenoid. On the trunk there were fifteen or sixteen scales in each transverse series, with the lateral line passing through the tenth or eleventh scale above the ventral border. It is not possible to see whether ventral ridge scales were present. The lateral line scales are not enlarged or thickened. Scales cover the cheek, the postero-lateral parts of the skull roof and the antero-dorsal corner of the opercular.

AFFINITIES. Although this species is known only by a single poorly preserved and very incomplete specimen it shows some points of interest. The specimen is shown to be a member of the Berycoidei by the combination of an orbitosphenoid, two supramaxillae, a pelvic with a spine and six soft rays, and dorsal fin spines. Within the Berycoidei the form of the skull roof, with a small supratemporal fossa, a largely enclosed supraorbital sensory canal with only a small median mucus cavity, and various other resemblances to the Cretaceous holocentrids *Caproberyx* and *Stichocentrus*, show it to be a member of the Holocentridae. The specimen differs from all other Holocentridae in having only six dorsal fin spines, with the sixth the longest, but in this it is close to *Caproberyx*, in both species of which (*C. superbus* (Dixon) and *C. polydesmus* (Arambourg)) there are seven dorsal spines. Among other resemblances to *Caproberyx* the most striking is the form of the infraorbitals, with the lachrymal sending back a long process along the entire length of the first infraorbital (the lachrymal is similar in *Trachichthyoides*). Less important resemblances to *Caproberyx* include the form of the posterior part of the skull roof (see p. 98), the proportions of the maxilla and premaxilla, the opercular ornament and the presence of epipleurals. All these characters are in contrast with *Stichocentrus*, but there are others in which the specimen resembles *Stichocentrus* and differs from *Caproberyx*. These include the roofed median mucus cavity and the simple, non-tubular posterior infraorbitals. Apart from these characters shared with either *Caproberyx* or *Stichocentrus*, the skull roof and superficial bones of the skull in general are less

strongly ornamented than they are in any other holocentrid, living or fossil, the posterior branch of the infraorbital sensory canal is more complex than it is in *Caproberyx* and *Stichocentrus*, there is an extensive contact between the parietal and pterotic in the wall of the post-temporal fossa, a character otherwise known in holocentrids only in *Trachichthyoides*, and there are only six soft rays in the pelvic fin, a difference from all other holocentrids and a resemblance to Trachichthyidae. Reviewing these various similarities and differences, I think it possible that the species represents a new genus, resembling *Caproberyx* in many characters, *Stichocentrus* in a few, and being more primitive than either in others. But I am unwilling to erect a new genus on such fragmentary material and pending the discovery of more complete specimens refer the species provisionally to *Caproberyx*.

V. DISCUSSION

There are described in this paper four berycoids, three from Cenomanian beds (Hakel & Hajula) and one from Senonian (Sahel Alma), representing three new genera and possibly four. Apart from increasing the number of known Cretaceous berycoid genera by 50% these new forms show certain features bearing on the origin and evolution of the Berycoidei.

(i) Distinction between families in Cretaceous Berycoidei

All known Cretaceous Berycoidei can be placed in either the Trachichthyidae (*Hoplopteryx, Acrogaster, Tubantia, Lissoberyx, Gnathoberyx*) or the Holocentridae (*Caproberyx, Trachichthyoides, Kansius, Stichocentrus*). But as has been shown above (pp. 80, 97) separation of these families becomes increasingly difficult as more Cretaceous forms are described. This is borne out by a list of the characters in which the two families are held to differ in the most recent diagnoses (Patterson, 1964 : 304, 341) :

(i) In Trachichthyidae there are fewer dorsal spines. But in the holocentrid *Caproberyx* the number of dorsal spines falls to 6–7, less than in many living and some fossil trachichthyids ; and in *Caproberyx* the spines are not inclined alternately to left and right as they are in most holocentrids.

(ii) The pelvic fins have six soft rays in Trachichthyidae, seven in Holocentridae. But in the holocentrid *Caproberyx pharsus* (p. 102) there appear to be only six soft rays (this conclusion is based only on one specimen, but in it the pelvic fin is well preserved).

(iii) In Trachichthyidae the skull roof bears high crests separating large mucus cavities, in Holocentridae broad ridges separating small mucus cavities. But in the trachichthyid *Lissoberyx* the skull roof is without crests or mucus cavities and has a sensory canal pattern very like that in the holocentrid *Myripristis*.

(iv) In Trachichthyidae the supratemporal fossa is large, in Holocentridae the frontals extend posteriorly and the fossa is small. But in the trachichthyid *Lissoberyx* the supratemporal fossa is of moderate size, intermediate between those of *Hoplopteryx* (Trachichthyidae) and *Caproberyx* (Holocentridae).

(v) In Trachichthyidae the mesethmoid is reduced. But in *Lissoberyx* the mesethmoid is not much reduced and approaches those of holocentrids in size.

(vi) The infraorbitals are deep in Trachichthyidae, shallow in Holocentridae. This difference still holds good for the Cretaceous genera, but in the living holocentrids *Plectrypops* and *Holotrachys* the infraorbitals are deeper than the lachrymal, just as they are in most trachichthyids.

(vii) The subocular shelf extends along all the infraorbitals in Holocentridae but is confined to the second infraorbital in Trachichthyidae. This difference still seems to hold good, although there is no subocular shelf on the first infraorbital in the holocentrids *Stichocentrus* and *Trachichthyoides*.

(viii) In Trachichthyidae the gape is large and the maxilla is not much expanded posteriorly, in Holocentridae the gape is smaller and the maxilla is expanded. But in the trachichthyids *Lissoberyx* and, in particular, *Gnathoberyx* there is no significant difference from holocentrids.

(ix) In Holocentridae there are scales on the anterior part of the opercular, in Trachichthyidae the opercular is without scales. But in the trachichthyid *Hoplopteryx lewisi* there is at least one large scale on the antero-dorsal part of the opercular, and in *Lissoberyx* the opercular is almost completely scaled.

Some of the features which differentiate living members of the Trachichthyidae and Holocentridae are already known to fail in Cretaceous genera (two supramaxillae in Holocentridae, one in Trachichthyidae; antorbital present in Holocentridae, absent in Trachichthyidae; ventral ridge scales present in Trachichthyidae, absent in Holocentridae: see Patterson, 1964), but the new forms described here show that almost all the differences between the two families no longer hold good. From a purely taxonomic point of view the exceptions listed above make it very difficult to provide adequate diagnoses of the two families, but since there is rarely any difficulty in deciding to which of the families any particular form belongs (see p. 80) there is little point in modifying the familial diagnoses by listing exceptions to every character. From a more general standpoint the Cretaceous Berycoidei give an excellent and well documented picture of the early evolution of a group. Today the Trachichthyidae and Holocentridae are well separated, moderately successful groups, the first containing bathypelagic fishes of wide distribution, the second neritic fishes of the tropics and sub-tropics. The trachichthyids also seem to be the stem group of a number of bathypelagic (Melamphaeidae, Stephanoberycidae, Gibberichthyidae, Korsogasteridae, Berycidae, Anoplogasteridae, Diretmidae) and neritic (Monocentridae, Anomalopidae) families, some of which were already differentiated in the Eocene (Berycidae, Monocentridae; Casier, 1966), others in the Miocene (Melamphaeidae, Ebeling, 1962), but most of which are without fossil record. The Trachichthyidae and Holocentridae can both be traced back to the Cenomanian, but in the Upper Cretaceous the two families converge strongly, with a blurring of the distinctions between them. This shows that in the Upper Cretaceous the " trachichthyid " and " holocentrid " facies had not yet become fully established, the Cretaceous fauna consisting of forms showing " experimental " combinations of characters. Simpson (1953 : 340–349) gives an excellent account of similar cases, mainly in mammals, and rightly comments on the difficulties of attempts to cram the early, diverging members of phyletic lines into higher categories (in this case families) based on what these lines are later to become.
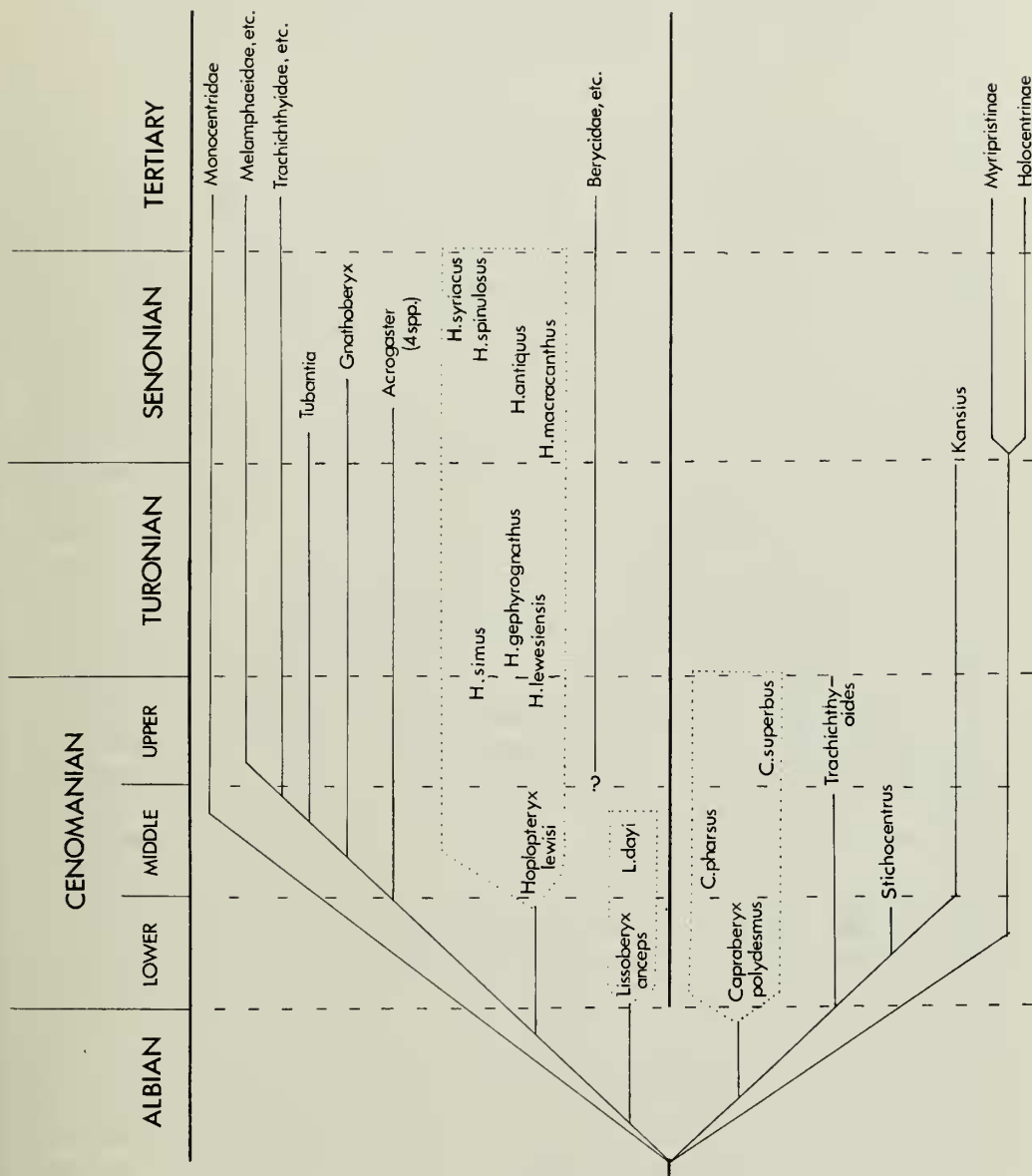
Fig. 11. A diagram suggesting the probable interrelationships of the known Cretaceous Trachichthyidae (left) and Holocentridae (right) and the living families of Berycoidei. Distance from the central, vertical line indicates degree of divergence from the common ancestor of the Berycoidei.

My present opinion of the interrelationships of the known Cretaceous Berycoidei is summarized in Text-fig. 11. General features worth noting in the early history of this suborder are the mosaic nature of the character combinations in the early forms and the fact that no genus seems to provide an entirely adequate ancestor for any later genus.

(ii) The Origin of the Berycoidei

We have seen that in the Cenomanian the Berycoidei were a group of recent origin in which much variation occurred. These early berycoids also exhibit a number of primitive characters which are absent or rare in Tertiary and living berycoids, including a toothed maxilla (*Gnathoberyx, Hoplopteryx macracanthus, Myripristis*) a partially roofed post-temporal fossa (*Hoplopteryx, Lissoberyx, Trachichthyoides, Caproberyx pharsus*) and an antorbital (*Hoplopteryx*, living holocentrids). In particular, *Lissoberyx* is a form which must lie very close to the origin of the suborder, sharing many characters of Trachichthyidae and Holocentridae. The primitive features of *Lissoberyx* have some bearing on the origin of the order Beryciformes as a whole, a question which I have discussed at some length (Patterson, 1964 : 459). I thought then that the Beryciformes might be diphyletic, the Berycoidei having an origin independent of the other two suborders, because I could see no convergence towards a common type between the two main suborders, Polymixioidei and Berycoidei, as they were traced back towards their first appearance in the Cenomanian, although there is good evidence of convergence towards a basal type within each suborder. While this is still true of the major characters separating the two suborders (caudal formula and presence or absence of a pelvic spine, epineurals and endopterygoid teeth), *Lissoberyx* is a berycoid which tends towards the polymixioids in the absence of ornament on the bones of the head, the smooth skull roof without mucus cavities, the high supraoccipital crest (all characters which I have used in separating the two suborders : Patterson, 1964 : 433), and in the completely scaled opercular. In all these characters *Lissoberyx* also resembles the four monotypic Cretaceous families placed in the suborder Dinopterygoidei (Patterson, 1964 : 434). The structure of *Lissoberyx* therefore increases the possibility that the Beryciformes is a monophyletic order and suggests that the ancestral form would have been a small fish with a smooth skull roof, a high supraoccipital crest arising from a moderately large supratemporal fossa, no ornament on the bones of the head, a reduced antorbital, a toothed maxilla, a scaly operculum and a partial roof to the post-temporal fossa. Only the last of these points excludes the Ctenothrissiformes from the direct ancestry of the group.

One or two other points in the anatomy of the Cretaceous Berycoidei are worth discussing briefly. All known Cretaceous Beryciformes, both polymixioids and berycoids, have a very constant sensory canal pattern on the skull roof : the main features of this pattern are a well developed parietal branch of the supraorbital canal extending back to open at the hind end of the frontal, usually into a depression on the parietal, this branch often being subdivided (into five branches in *Berycopsis* and *Homonotichthys*, four in *Caproberyx pharsus*, etc.), a medial branch meeting its fellow in a median depression over the orbit, and a lateral branch over the anterior part of

the orbit. This pattern of the supraorbital canal seems to be very widely distributed among primitive teleosts, although Gosline, Marshall & Mead (1966 : 3) find that the medial branches fail to meet in a cross-commissure in " isospondylous " fishes. An exactly similar pattern occurs in the Ctenothrissiformes, except that in *Aulolepis* the parietal branch is reduced and does not reach the parietal. A well developed parietal branch of the supraorbital canal, terminating in or near the parietal, is generally held to be a relic of the posterior part of the supraorbital canal and the anterior pit-line of halecostomes and more primitive actinopterygians. Arambourg (1950 ; 1954 : 34, 72) considers that such parietal branches occur only in the most primitive teleosts (*Clupavus*, *Thrissopater*) but my own observations suggest that they are more widely distributed, although it is doubtful whether the parietal branches are strictly primary or even homologous in all teleosts.

The subocular shelf has been shown by Smith & Bailey (1962) to be an important taxonomic feature. Among living teleosts a subocular shelf occurs only in the Acanthopterygii (*sensu* Greenwood *et al.*, 1966) and in the osteoglossiform family Notopteridae (Greenwood *et al.*, 1966 : 363), where it is undoubtedly developed independently. There is also a subocular shelf in all the Cretaceous Beryciformes. Otherwise, a subocular shelf is only known to occur in the Cretaceous ctenothrissiform *Ctenothrissa* (Patterson, 1964 : 229), where there is a narrow shelf on the first and anterior part of the second infraorbitals. This is powerful additional evidence for close relationship between the Ctenothrissiformes and the ancestral Beryciformes.

The presence of scales on the opercular is undoubtedly an advanced character in actinopterygians since scales could not develop over the dermal opercular until it had lost its covering of enameloid tissue, which can develop only in contact with the ectoderm. The opercular is without scales in all elopomorph, clupeomorph and osteoglossomorph teleosts, and in protacanthopterygian teleosts opercular scales are only present below the myctophoid level in esocoids and alepocephaloids. In Beryciformes the occurrence of a completely scaled opercular in Cretaceous and living polymixioids, in dinopterygoids and in *Lissoberyx* strongly suggests that this feature is primitive for the order, and presumably for all acanthopterygians. This hypothesis receives support from the completely scaled opercular of the Ctenothrissiformes *Aulolepis*, *Pateroperca* and the Lebanese species of *Ctenothrissa*. In Berycoidei scales are absent on the opercular in all Trachichthyidae except *Lissoberyx* and *Hoplopteryx lewisi* while in Holocentridae the opercular is only scaled anteriorly. These are clearly cases of secondary reduction from a complete scale covering, evidently associated with the development of spiny ornament on the opercular. An analogous situation occurs in the Ctenothrissiformes, where *Ctenothrissa microcephala* and *C. radians* show progressive reduction in the scaling of the opercular associated with increased ornamentation.

A common ancestor of the three suborders of Beryciformes, all of which are present and clearly distinct in the Cenomanian, must have lived in the Albian or earlier. It is worth briefly reviewing the few records of supposed Beryciformes in pre-Cenomanian beds. Weiler (1947) referred to the Berycomorphi isolated scales and a pelvic fin from the Upper Aptian of Armenkov Island, S. Georgia. These specimens have not been figured and the scales, which were very briefly described,

are evidently without clearly diagnostic features. The pelvic fin is described as containing a short, slender spine, one unbranched soft ray and six branched rays. These specimens seem doubtful evidence of Beryciformes in the Aptian. Much earlier in time, beryciform otoliths have been described from the Tithonian and Wealden of Germany (Martin & Weiler, 1954, 1957). These Jurassic and Wealden otoliths must be treated with some reserve : since otoliths can at present only be identified by comparison with living forms the accuracy of otolith determinations must decrease with increasing age.

In the Gault of S.E. England (at Small Dole, near Henfield, Sussex, Ford Place, Wrotham, Kent, and King's Lynn, Norfolk) there occur fragmentary remains of two small teleosts, one with ctenoid scales bearing parallel rows of small, flat spines which resemble those of *Ctenothrissa* and some berycoids, the other with scales in which the exposed circuli are broken up into very small tubercles. As yet, I have seen no fin spines or other structures diagnostic of Beryciformes with these fragments, but various skull bones are very suggestive of the Ctenothrissiformes and Beryciformes. The first of these small teleosts appears to have a toothed maxilla and two very small patches of teeth on the endopterygoid : the second has a broad, cavernous premaxilla of typical trachichthyid type. Since fragments of these small fishes are not uncommon at certain horizons in the Middle Gault it may eventually prove possible to give an account of Beryciformes in the Middle Albian.

VI. REFERENCES

Arambourg, C. 1950. Nouvelles observations sur les Halécostomes et l'origine des Clupeidae. *C.R. Acad. Sci.*, Paris, **231** : 416–418, 1 fig.

—— 1954. Les poissons crétacés du Jebel Tselfat (Maroc). *Notes Mém. Serv. géol. Maroc,* Rabat, **118** : 1–188, 20 pls.

Bardack, D. 1965. Anatomy and evolution of chirocentrid fishes. *Paleont. Contr. Univ. Kans.*, Topeka, Vertebrata **10** : 1–88, pls. 1, 2.

Brongersma-Sanders, M. 1957. Mass Mortality in the Sea. *Mem. Geol. Soc. Amer.*, Washington, **67**, 1 : 941–1,010, 7 figs.

Casier, E. 1966. *Faune ichthyologique du London Clay.* xiv + 496 pp., 68 pls. Brit. Mus. (Nat. Hist.), London.

Conrad, G. M. 1941. A fossil squirrel-fish from the Upper Eocene of Florida. *Geol. Bull. Dept. Conservation, Florida,* Tallahassee, **22** : 5–25, 3 pls.

Dunkle, D. H. & Olsen, S. J. 1959. Description of a beryciform fish from the Oligocene of Florida. *Spec. Publs Fla geol. Surv.*, Tallahassee, **2** : 1–20, 4 figs.

Dubertret, L. 1963. Liban et Syrie. *Lexique Strat. Int.*, Paris, **3**, 10cl : 7–155, 3 pls.

Ebeling, A. W. 1962. *Scopelogadus* (?) *capistraensis*, a new fossil melamphaid (Pisces, Teleostei) from Capistrano Beach, California. *Postilla*, New Haven, **71** : 1–6, 1 fig.

d'Erasmo, G. 1922. Catalogo dei Pesci fossili della Tre Venezie. *Memorie Ist. geol. miner. Univ. Padova,* **6** : 1–181, 6 pls.

—— 1946. L'ittiofauna cretacea di Comeno nel Carso triestino. *Atti Accad. Sci. fis. mat. Napoli* (3a) **2**, 8 : 1–136, 1 pl.

Gosline, W. A. 1961. Some osteological features of modern lower teleostean fishes. *Smithson, Misc. Coll.*, Washington, **142**, 3 : 1–42, 8 figs.

—— 1963. Considerations regarding the relationships of the percopsiform, cyprinodontiform, and gadiform fishes. *Occ. Pap. Mus. Zool. Univ. Mich.*, Ann Arbor, **629** : 1–38, 11 figs.

Gosline, W. A., Marshall, N. B. & Mead, G. W. 1966. Iniomi. Characters and Synopsis of Families. *Mem. Sears Fdn. mar. Res.*, New Haven, **1**, 5 : 1–18, figs. 1–6.

GREENWOOD, P. H., ROSEN, D. E., WEITZMAN, S. H. & MYERS, G. S. 1966. Phyletic studies of Teleostean Fishes, with a provisional Classification of Living Forms. *Bull. Amer. Mus. Nat. Hist.*, New York, **131** : 339–456, pls. 21–23, 32 charts.

HAY, O. P. 1903. On a collection of Upper Cretaceous fishes from Mount Lebanon, Syria, with descriptions of four new genera and nineteen new species. *Bull. Amer. Mus. Nat. Hist.*, New York, **19** : 395–452, 14 pls.

HUSSAKOF, L. 1929. A new teleostean fish from the Niobrara of Kansas. *Amer. Mus. Novit.*, New York, **357** : 1–4, 2 figs.

KRAMBERGER, C. G-. 1895. De Piscibus fossilibus Comeni, Mrzleci, Lesinae et M. Libanonis. *Djela jugosl. Akad. Znan. Umjetn.*, Zagreb, **16** : 1–67, 12 pls.

MARSHALL, N. B. 1961. A young *Macristium* and the Ctenothrissid fishes, *Bull. Br. Mus. nat. Hist.* (Zool.), London, **7** : 353–370, 4 figs.

MARTIN, G. H. 1920. *Anguillavus hackberryensis*, a new species and a new genus of fish from the Niobrara Cretaceous of Kansas. *Kans. Univ. Sci. Bull.*, Lawrence, **13** : 95–97, pl. 6.

MARTIN, G. P. R. & WEILER, W. 1954. Fisch-Otolithen aus dem deutschen Mesozoikum (Dogger bis Wealden). *Senck. leth.*, Frankfurt a.M., **35** : 119–192, pls. 1–4.

—— 1957. Das Aldorfer Otolithen-" Pflaster " und seine Fauna. *Senck. leth.*, Frankfurt a.M., **38** : 211–250, pls. 1–3.

NELSON, E. M. 1955. The Morphology of the Swim Bladder and Auditory Bulla in the Holocentridae. *Fieldiana, Zool.*, Chicago, **37** : 121–130, 3 pls.

PATTERSON, C. 1964. A review of Mesozoic acanthopterygian fishes, with special reference to those of the English Chalk. *Phil. Trans.*, London (B) **247** : 213–482, pls. 2–5.

—— 1967. A second specimen of the Cretaceous teleost *Protobrama* and the relationships of the sub-order Tselfatioidei. *Ark. Zool.*, Stockholm, **19:** 215–234, 8 figs.

PICTET, F. J. & HUMBERT, A. 1866. *Nouvelles récherches sur les poissons fossiles du Mont Liban.* vii + 114 pp., 19 pls. Genève.

REGAN, C. TATE. 1911. The anatomy and classification of the Teleostean fishes of the orders Berycomorphi and Xenoberyces. *Ann. Mag. Nat. Hist.*, London (8) **7** : 1–9, 1 pl.

ROGER, J. 1946. Les invertébrés des couches à poissons du Crétacé supérieur du Liban. *Mém. Soc. géol. Fr.*, Paris, **23**, 2 : 1–92, 10 pls.

ROSEN, D. E. 1964. The relationships and taxonomic position of the halfbeaks, killifishes, silversides, and their relatives. *Bull. Amer. Mus. Nat. Hist.*, New York, **127** : 217–268, pls. 14, 15.

SIMPSON, G. G. 1953. *The Major Features of Evolution.* xx + 434 pp., 52 figs. Columbia University, New York.

SMITH, C. L. & BAILEY, R. M. 1961. Evolution of the dorsal-fin supports of percoid fishes. *Pap. Mich. Acad. Sci.*, Ann Arbor, **46** : 345–364, 1 pl.

—— 1962. The Subocular Shelf of Fishes. *J. Morph.*, Philadelphia, **110** : 1–17, pls. 1–3.

STARKS, E. C. 1904. The osteology of some Berycoid fishes. *Proc. U.S. Nat. Mus.*, Washington, **27** : 601–619, 9 figs.

WEILER, W. 1947. Fische, pp. 17–18 *in* Wilckens, O. Paläontologische und geologische Ergebnisse der Reise von Kohl-Larsen (1928–29) nach Sud-Georgien. *Abh. senckenb. naturforsch. Ges.*, Frankfurt a.M., **474** : 1–75, 7 pls.

WOODWARD, A. SMITH. 1901. *Catalogue of the fossil fishes in the British Museum (Natural History)*, **4.** xxxviii + 636 pp., 19 pls. Brit. Mus. (Nat. Hist.), London.

—— 1902. The fossil fishes of the English Chalk. Part I. *Mon. Palaeontogr. Soc.*, London, **1902** : 1–56, pls. 1–13.

—— 1942. Some new and little-known Upper Cretaceous fishes from Mount Lebanon. *Ann. Mag. Nat. Hist.*, London (11) **9** : 537–568, 5 pls.